

THE CRETACEOUS DECAPOD CRUSTACEA OF ARGENTINA AND THE ANTARCTIC PENINSULA

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ABSTRACT. Decapod crustaceans are widespread in Cretaceous rocks of the mainly marine Mesozoic Neuquén, and Austral or Magallanes basins of continental Argentina as well as in western Antarctica. The Glypheidae are represented by *Glypheia* sp. from the Neocomian of the Neuquén basin and *G. oculata* Woods from the Santonian of the Austral basin. *Meyerella rapax* (Harbort) is described from the late Valanginian–early Hauterivian of the Neuquén basin. *Palaeastacus terraereginae* (Etheridge), *P. sussexiensis* (Mantell), *Eryma* sp. cf. *E. sulcata* Harbort and *Enoplocyrtia* sp. represent the erymids. *Hoploparia longimana* (Sowerby), *H. antarctica* Wilckens, *H. stokesi* (Weller), *H. arbei* sp. nov., and *H. sp. A* and *B* are also described and figured. Callianassids are represented by three species: *Protocallianassa patagonica* Aguirre Urreta from the early Cretaceous of the Austral basin, *Callianassa meridionalis* Ball from the late Cretaceous of Antarctica and *C. burckhardtii* Böhm from the Cretaceous–Tertiary boundary of the Neuquén basin, associated with trace fossils of the ichnogenus *Thalassinoides*. No brachyurans are presently known in Cretaceous rocks of Argentina. Four paleogeographic reconstructions from the late Jurassic to the early Tertiary depict the stratigraphic and geographic distributions of the genera studied.

REMAINS of decapod crustaceans have been known in Cretaceous rocks of Argentina since the beginning of the century. Such remains were very scarce and consist of fragmentary specimens recovered from isolated localities of the Austral and Neuquén basins, as well as from Antarctica. During the last ten years our knowledge of the Cretaceous decapod fauna has notably increased due to extensive collecting. The purposes of this paper are to describe the Cretaceous decapod crustaceans of Argentina, mainly based on personal collections, to supplement previous descriptions, and to provide illustrations of well-preserved material.

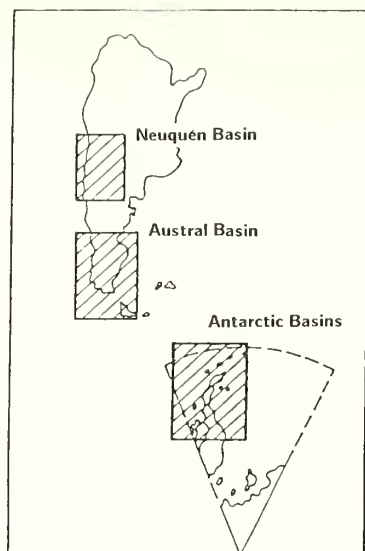
GEOLOGY

Geological setting

The decapod crustaceans described from the main Cretaceous marine basins of Argentina (text-fig. 1) are from the Neuquén and Austral (or Magallanes) basins and from the Antarctic region, at that time part of a continuous foreland connecting the Antarctic Peninsula with the Patagonian terrains (Dalziel 1974).

Neuquén basin. This basin has thick marine Mesozoic sequences derived from successive Pacific transgressions which are closely related to the evolution of the Andes between latitudes 32° and 39° S (text-fig. 2). The Early Cretaceous marine sequence comprises the Mendoza Group and consists of black shales (Vaca Muerta Formation; Tithonian–Berriasian), thinly laminated limestones (Quintuco Formation; Berriasian–Valanginian), sandstones and shales (Mulichinco Formation; Berriasian–Valanginian) and limestones and shales (Agrio Formation; Hauterivian–Barremian) (see Digregorio and Uliana 1979). The Valanginian sequence of the southern Mendoza sector is represented by thick carbonate deposits of the Chachao Formation (Uliana *et al.* 1979) (see text-fig. 3).

The Late Cretaceous marine sequence of the Malargüe Group overlies the continental deposits of Rayoso and Neuquén Groups. The former is composed at the base of brackish water shales



TEXT-FIG. 1. Location of the studied areas. Rectangles indicate text-figs. 2, 4 and 5.

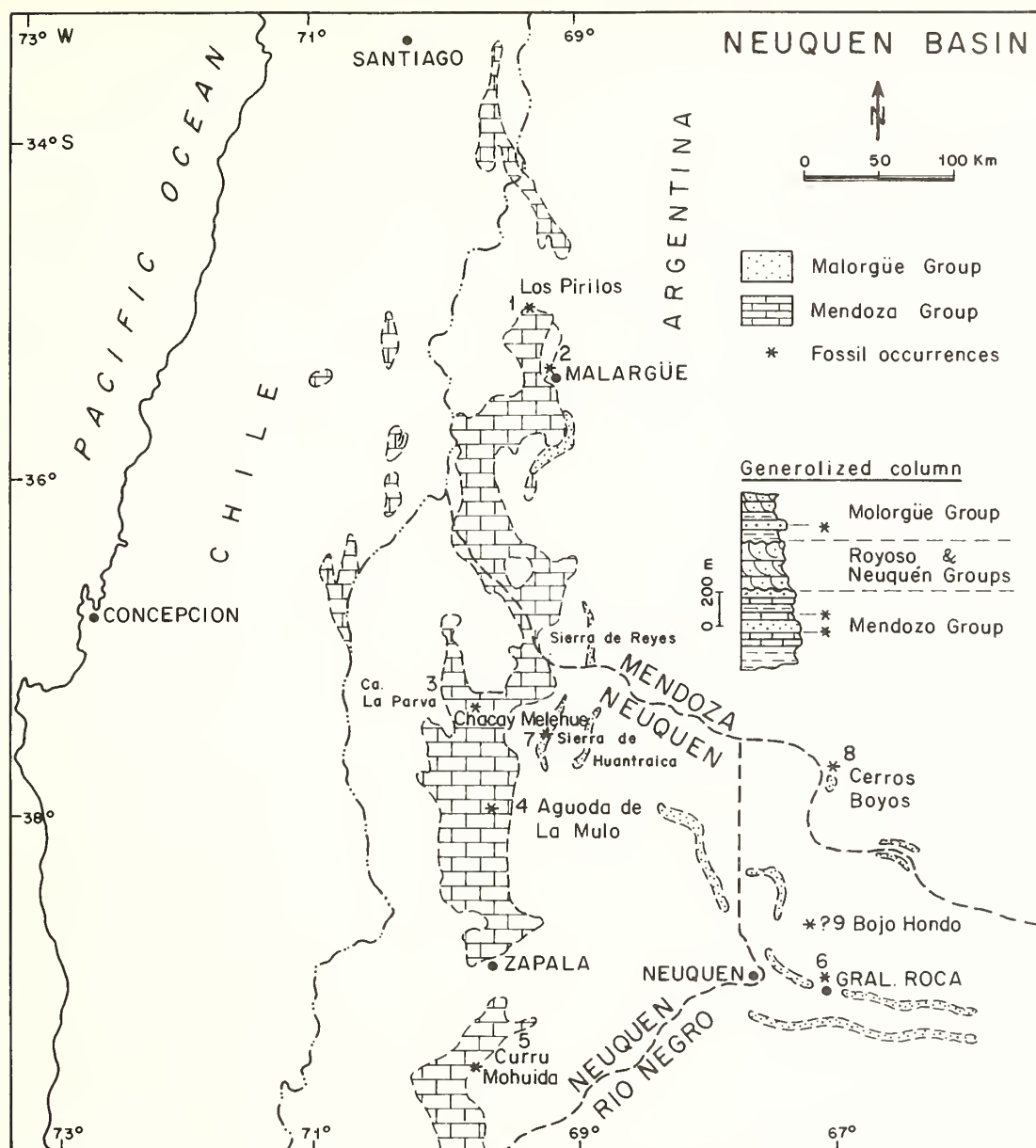
(Loncoche Formation), marine sandstones and shales (Roca Formation) and continental red beds (Pircala Formation). The Roca Formation represents the first Atlantic transgression following the opening of the South Atlantic at these latitudes (Weaver 1927).

Austral Basin. This basin is developed south of latitude 45° S and contains a lower section derived from a Pacific transgression, and an upper section connected with the South Atlantic. This last seaway was established after the Cenomanian (Camacho 1967) (text-fig. 4). The lowest part of the section is represented by the Pueyrredón Group, which is comprised of basal sandstones of the Springhill Formation (Tithonian–early Valanginian), black shales of the Río Mayer Formation (Berriasian–late Albian) and sandstones which mark the slow regression of the Cretaceous seas to the south (Hatcher 1900; Aguirre Urreta and Ramos 1981*b*). These sandstones are represented in the northern part of the basin by the Río Belgrano Formation (Barremian–early Aptian), by the Kachaike Formation (Albian–Cenomanian) of the San Martín Lake area; and by the Piedra Clavada Formation (Albian–Cenomanian) of the Cardiel Lake region (Riccardi 1971; Ramos 1982).

The sequence of turbidites of the Cerro Toro Formation is deposited over the black shales of the Río Mayer Formation at the middle inner part of the basin (Riccardi and Rolleri 1980). The eastern southern part of the basin is represented by regressive sandstones and shales of the Puesto El Alamo Formation (Cenomanian–Coniacian), Mata Amarilla Formation (Coniacian–Santonian) and Cerro Cazador Formation (Campanian–Maastrichtian) (see Leanza 1972; Nullo *et al.* 1981*a* and *b*; Malumíán *et al.* 1983; Riccardi 1988; Riccardi and Aguirre Urreta 1988; text-fig. 3).

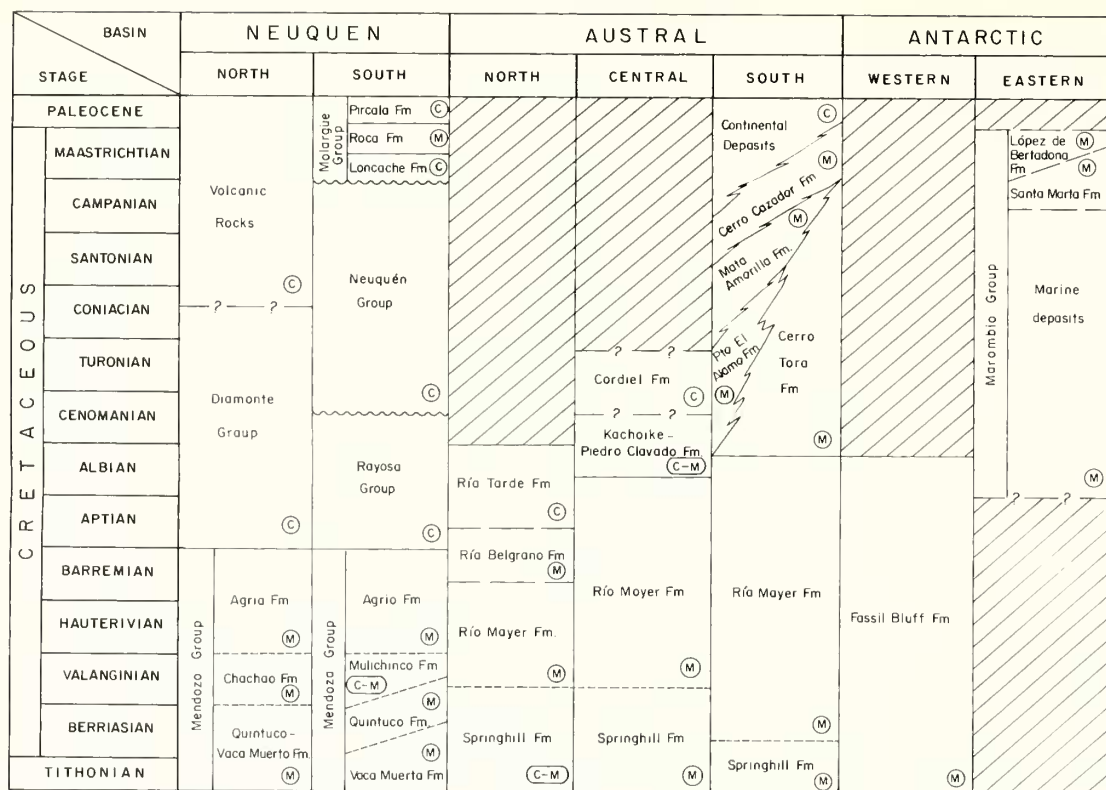
Antarctic Sector. Two different basins can be distinguished in the Antarctic Peninsula during the Mesozoic with diverse geologic evolution; the eastern forearc and western retroarc basins (Thomson 1983; text-fig. 5). The western basin encompasses the terrains adjacent to Alexander Island (70° to 72° S), where mainly marine clastic sequences of late Jurassic to Albian age are exposed. The Fossil Bluff Formation consists of mudstones with a smaller amount of sandstones and conglomerates (Thomson 1983).

The Eastern basin is well developed at the northeastern extremity of the Antarctic Peninsula in James Ross, Snow Hill, Vega, Seymour (Vicecomodoro Marambio in the Argentina literature) and adjacent islands (63° to 65° S). The Upper Cretaceous marine fossiliferous sequence (Santa Marta



TEXT-FIG. 2. Distribution of Cretaceous outcrops in the Neuquén Basin. Fossil localities with decapod crustaceans cited in the text and a generalized stratigraphic column are also shown. (Base map from Riccardi 1983.)

and López de Bertodano formations) consists of siltstones, shales with calcareous nodules, sandstones and conglomerates. A Campanian–Maastrichtian age is assigned to these formations based on the invertebrate and microplankton assemblages (Palamarczuk *et al.* 1984; Macellari 1986; Olivero *et al.* 1986; text-fig. 3).



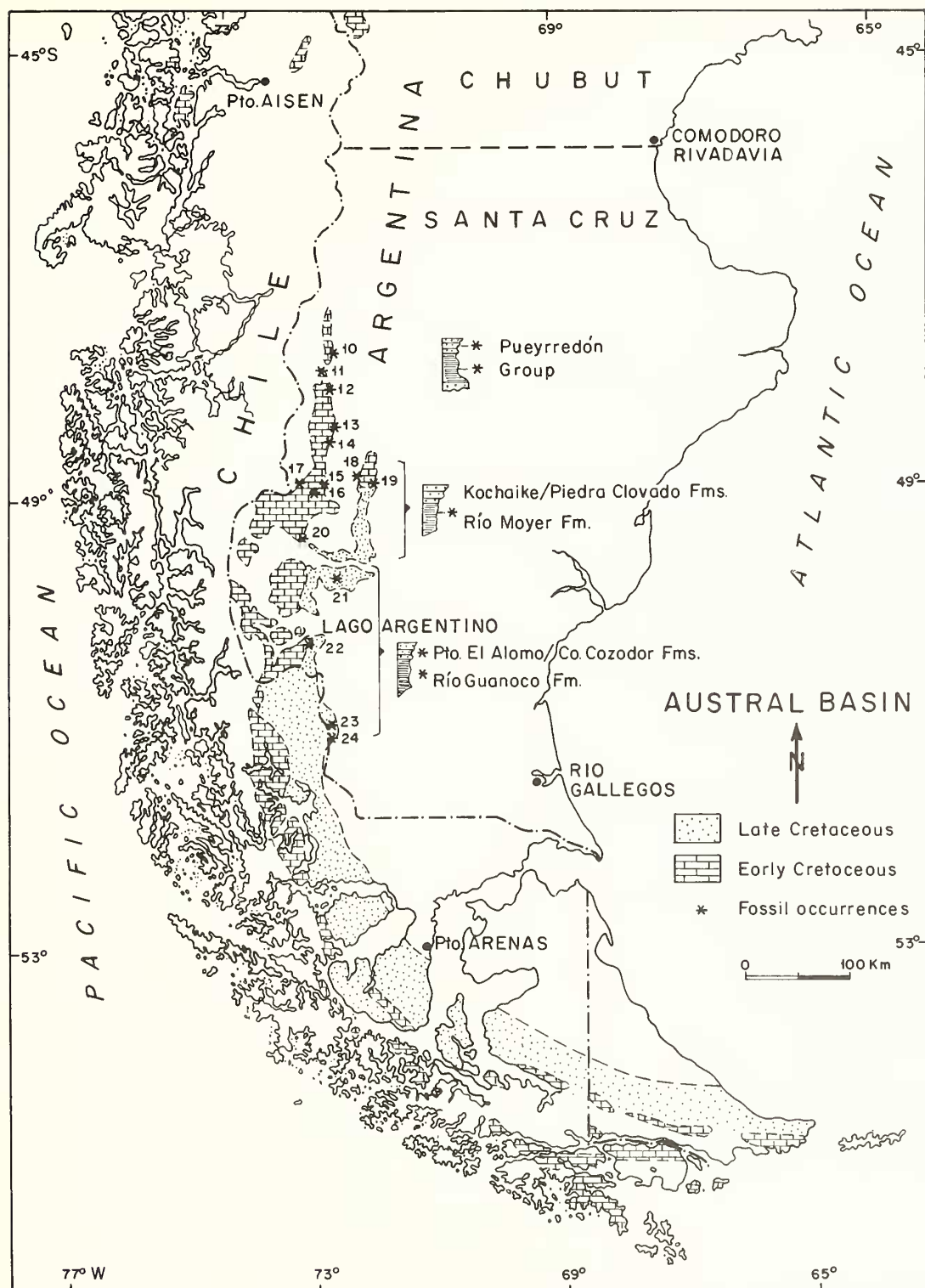
TEXT-FIG. 3. Stratigraphic chart for the Neuquén, Austral and Antarctic basins during the Cretaceous.

FOSSIL LOCALITIES

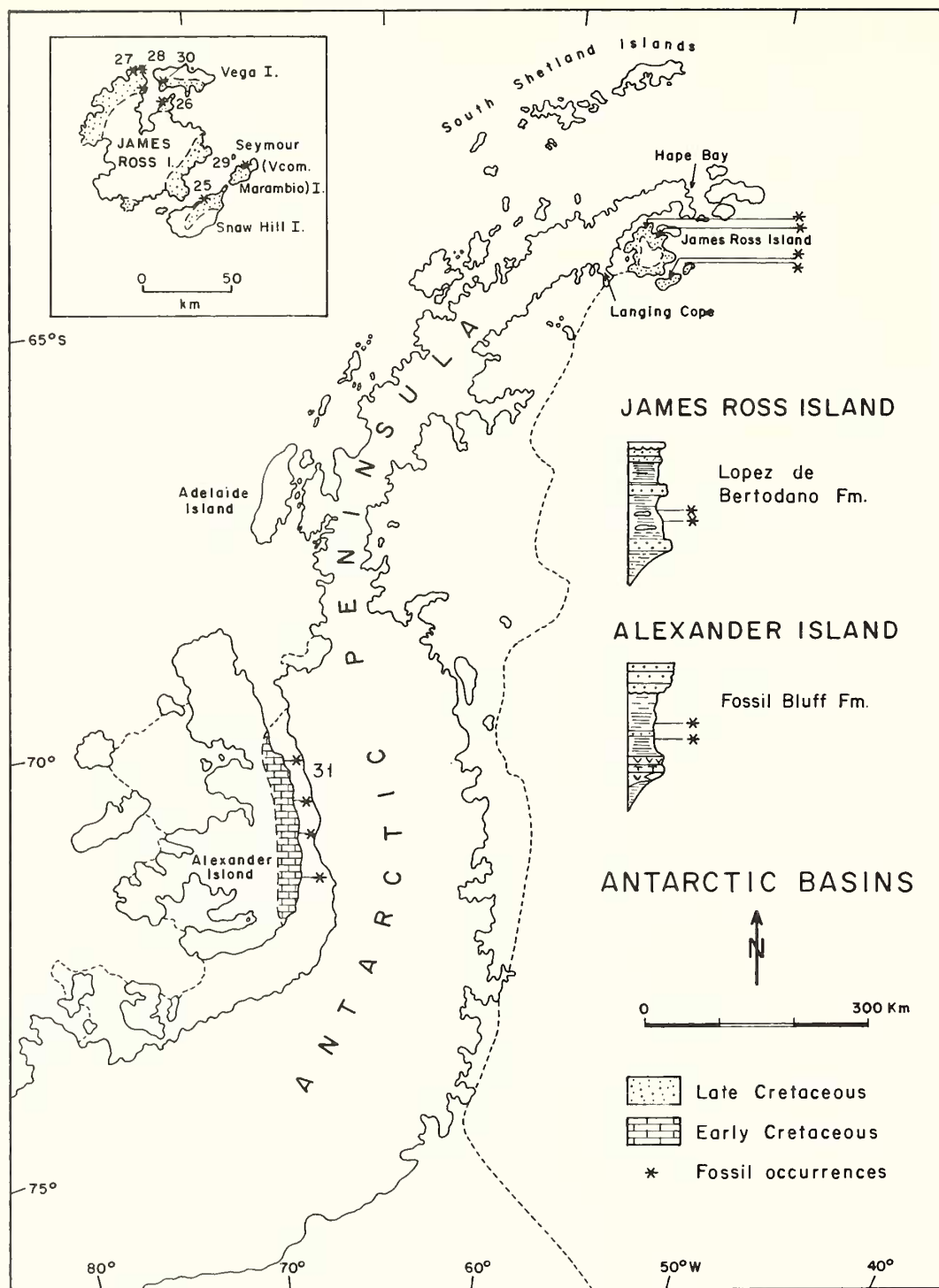
All fossil localities are indicated by numbers in the following text and on text-figs. 2, 4 and 5.

Neuquén basin (provinces of Mendoza, Neuquén, Río Negro and La Pampa; text-fig. 2)

1. *Los Pirilos*. This locality is located on the access to Baños de Chachao from highway 40, in discontinuous outcrops of the Chachao Formation. Damborenea *et al.* (1979) described *Callianassa* aff. *peruviana* from these beds dated as late Berrasian to early Valanginian.
2. *Malargüe*. Three specimens of *Callianassa* sp. are deposited in the collections of Museo de La Plata which were collected from the Malargüe Formation, dated as Maastrichtian by Bertels (1969).
3. *Cerro La Parva*. This locality, situated east of Chacay Melhue, is where Regairaz (1944) collected several specimens referred to *Meyerella rapax* (Harbort), from levels 3 and 5 of his profile X, in the Mulichinco Formation. They were associated with *Karakaschiceras attenuatus* (Behrendesen), an ammonite indicating a late Valanginian–early Hauterivian age (Riccardi *et al.* 1971; Riccardi 1984). I recently collected five more specimens of *M. rapax* from the same level and locality.
4. *Aguada de la Mula*. This locality is situated 8 km south of the village of Churriaca, on the western flank of Mula-Naunaucó anticline, near Pampa del Salado. A. Gutiérrez collected a specimen of *Glyphea* sp., from the upper Agrio Formation, above the highest level of *Crioceratites andinum* (Gerth), an ammonoid indicative of a late Hauterivian–early Barremian age (Riccardi 1984).
5. *Curru Mahuida*. This locality is situated 70 km south of the city of Zapala, in the area of Covunco centro. J. Frenguelli collected three fragmentary chelipeds here, assigned to *Hoploparia* sp. B. They were associated with *Thurmaniceras* sp., assigned to the Berriasian–early Valanginian (Frenguelli 1937; Riccardi 1984).
6. *General Roca*. General Roca is a classic locality of the Roca Formation, situated 2.5 km north of the city of General Roca. Böhm (1911) described and illustrated *Callianassa burckhardti* Böhm from the Danian beds



TEXT-FIG. 4. Distribution of Cretaceous outcrops in the Austral Basin. Fossil localities with decapod crustaceans cited in the text and three generalized stratigraphic columns are also shown. (Base map from Riccardi 1983.)



TEXT-FIG. 5. Distribution of Cretaceous outcrops in the Antarctic Peninsula and adjacent islands. Fossil localities with decapod crustaceans cited in the text and two generalized stratigraphic columns are also shown. Insert on the top left margin is a detail of the James Ross Island group. (Base map from Thomson 1983.)

of the formation. In other localities of the Neuquén basin, fragmentary chelae here referred to callianassids, have been collected by several workers (*Sierra de Huantraico* [7] Ramos (1981); *Cerro Bayos* [8] Leanza (1967); *Bajo Hondo* [9], Etchevehere (1950)); text-fig. 2) from both Maastrichtian and Danian beds.

Austral basin (province of Santa Cruz; text-fig. 4)

10. *Río Belgrano este*. This locality is situated on the east side of the Belgrano River, 1 km above its mouth in the extra-andean plains. A complete and articulated specimen of *Palaeastacus terraereginae* (Etheridge) was found together with abundant *Hatchericeras patagonense* (Stanton) and conspicuous bioturbation, in the Río Belgrano Formation. The age of this assemblage is Barremian.

11. *Lago Belgrano Sur*. This locality was discovered by Hauthal (in Feruglio 1949, p. 182) on the northern shore of Lake Belgrano. I collected one specimen of *Eryma* cf. *E. sulcata* Harbort from the Río Mayer Formation, associated with the ammonoids *Favrella americana* (Favre) and *Aegocrioceras* sp., indicating an upper early Hauterivian age (Riccardi 1984).

12. *Chorrillo Rivera*. This locality is situated approximately 7 km southeast of the mouth of Roble River in Lake Burmeister. Several fragmentary specimens of *P. terraereginae* (Etheridge) were collected from the Río Mayer and Río Belgrano formations, associated with the ammonoids *Hatchericeras patagonense* (Stanton) and *Cryptocrioceras yrigoyeni* (Leanza), indicating a Barremian age (Aguirre Urreta and Ramos 1981b).

13. *Chorrillo del Medio*. The locality is situated on the eastern bank of the Chorrillo (creek) del Medio, 5 km above its confluence with the Ñire River. A rich fauna composed of *P. terraereginae* (Etheridge), *Hoploparia longinana* (Sowerby), and *Protocallianassa patagonica* Aguirre Urreta was recovered from the upper part of the Río Mayer Formation, associated with the ammonoids *Colchidites vulanensis australis* Klinger, Kakabadze and Kennedy and *Sanmartinoceras africanum insignicostatum* Riccardi, Aguirre Urreta and Medina, indicating a late Barremian age (Aguirre Urreta and Klinger 1986; Riccardi *et al.* 1987).

14. *Loma Pelada*. This locality is situated 6 km north-northeast of Estancia Tucu-Tucu, on the top of a small hill known as Bald Mountain (Hatcher 1903). Aguirre Urreta (1983) illustrated specimens of *P. patagonica* associated with the same ammonoid fauna found at locality 13.

15. *Puesto Bajo Comisión*. This locality is situated on the south valley of Bajo Comisión Creek, tributary of the Fósiles River. A fragmentary specimen of *Enoplocyrtia* sp., recovered from the Río Mayer Formation, is associated with a rich assemblage of ammonoids including *Australiceras* (*A.*) *hallei* Aguirre Urreta, *Toxoceratoides nagerai* (Leanza) and *Sanmartinoceras walshense* (Etheridge) of late early Aptian age (Aguirre Urreta 1985a; 1986; Riccardi *et al.* 1987).

16. *La Muralla*. This locality is situated in the region of San Martín Lake, 1 km south-east of Puesto Bajo Comisión. I have collected three specimens of *P. terraereginae* (Etheridge) and one specimen of *Hoploparia* sp. A, associated with the ammonoid *Peltocrioceras deecke* (Favre), indicative of a late Aptian age (Aguirre Urreta 1985a) from the uppermost part of the Río Mayer Formation.

17. *La Señalada*. This locality is situated 4 km north of Estancia Sierra Nevada, near Lake San Martín. Three chelae of *Hoploparia* sp. A were collected from the upper Río Mayer Formation, associated with the ammonoids *P. deecke* (Favre) and *Helicanacylus patagonicus* (Stolley) indicating a late Aptian age (Aguirre Urreta 1985a; 1986).

18. *La Horqueta*. This locality discovered by Piatnitzky (1938), is located on Cardiel River, approximately 0.4 km west of its confluence with del Medio River. I have collected three chelae assigned to *Hoploparia* sp. A from the Río Mayer Formation, associated with *Australiceras* (*A.*) *hallei* and *Tropaeum* (*T.*) *inflatum* Aguirre Urreta spp., ammonoids indicating an Aptian age (Riccardi 1984; Aguirre Urreta 1985a).

19. *Río Cardiel*. This locality is situated on the southern slope of Karken Hill, on the northern margin of Cardiel River, 5 km upstream from its mouth in Cardiel Lake. Specimens of *Palaeastacus sussexiensis* (Mantell) (one specimen collected by F. Medina) were found in the fossiliferous upper part of the Río Mayer Formation, associated with *P. deecke* (Favre) from the late Aptian (Aguirre Urreta 1985a).

20. *Puesto El Alamo*. This locality is situated on the northern coast of Viedma Lake (Nullo *et al.* 1981a, locality 2 of fig. 1). Two specimens of *Hoploparia arbei* sp. nov. were collected by H. Arbe and a collection of more than 30 specimens was later made by A. Riccardi, H. Klinger and B. Aguirre Urreta from outcrops of the Puesto El Alamo Formation together with the ammonite *Placentoceras* Meek, indicating the Turonian–Coniacian boundary (Riccardi and Aguirre Urreta 1988).

21. *Bajo Cerro Indice*. This locality is situated near Indice Hill, south-east of Viedma Lake, where I collected four specimens of *Glyphca oculata* Woods from outcrops of the Mata Amarilla Formation in the same levels with *Baculites* cf. *kirki* Matsumoto, *Anagaudryceras* cf. *politissimum* (Kossmat) and *Polyptychoceras* (*P.*) sp., indicating a Santonian age (Riccardi and Aguirre Urreta 1988).

22. *Arroyo Centinela*. This locality is situated south of Argentino Lake (Nullo *et al.* 1981a, locality 14 of fig. 3) where Nañez collected four chelae of *Callianassa* sp. from outcrops of the Río Guanaco Formation (Nullo *et al.* 1981b) or the Cerro Toro Formation (Riccardi and Roller 1980) of late Santonian–early Campanian age based on its ammonite fauna (Nullo *et al.* 1981b).
23. *Cerro Cazador*. This classic locality of the Austral Basin is situated near Chile, 60 km south of the city of Río Turbio. Hauthal (in Wilckens 1907) collected the holotype of *Hoploparia antarctica* Wilckens from the Cerro Cazador Formation (level f) which is associated with *Hoplitoplacenticerus plasticus* (Pulchke), an ammonoid of late Campanian age (Riccardi 1984).
24. *Arroyo San José*. This locality is situated 6 km south of San José Creek, near the Estancia San José, in Sierra Dorotea. M. Hünicken collected a specimen of *H. antarctica* Wilckens from a horizon 55 m below the top of the Cerro Cazador Formation and assigned this level to the Campanian–earliest Maastrichtian (Hünicken 1955; Riccardi 1984).

Eastern Antarctic basin (text-fig. 5)

25. *Admiralty Sound (Estrecho Bouchard)*. The first description of Cretaceous decapods from Antarctica was that of '*Glypheus*' *stokesi* Weller from this locality, situated on the north-western coast of Snow Hill Island (Weller 1903; Ball 1960).
26. *Croft Bay*. Several localities are situated on the edges of Croft Bay, on the north east coast of James Ross Island. Remains of *Meyeria crofti* Ball, *Hoploparia stokesi* (Weller), and *Callianassa meridionalis* Ball are associated with ammonoids which indicate an early to middle Campanian age (Ball 1960).
27. *Brandy Bay (Bahía Bonita)*. Six specimens of *C. meridionalis* Ball described and illustrated herein were collected by E. Olivero from this locality, situated in the northern extremity of James Ross Island, associated with Campanian ammonoids of the *Baculites bailyi* zone (Olivero pers. comm. 1986).
28. *Bahía Santa Marta*. This locality is in a cove situated on the north-northeastern coast of James Ross Island. A. López Angrimm collected three specimens of *C. meridionalis* Ball from the Santa Marta Formation of ?Santonian–Campanian age (Olivero *et al.* 1986).
29. *Cabo Bodmann*. This locality is situated south-east of Bodmann Cape, on the northern coast of Seymour (Vicecomodoro Marambio) Island. Del Valle and Rinaldi (1975) described several specimens of *H. stokesi* (Weller) from this locality, associated with *Pachydiscus* aff. *gollevillensis* and *Maorites tuberculatus* of late Campanian age.
30. *Cabo Lamb*. This locality is situated in the southwestern extreme of Vega Island. Two specimens of *H. stokesi* (Weller) described here were collected by F. Medina and R. del Valle, from Campanian beds of the López de Bertodano Formation.

Western Antarctic basin (text-fig. 5)

31. *East Coast of Alexander Island*. A series of 13 localities with decapods is known from the east coast of the island. The age of the different assemblages ranges from the Berrasian to early Albian (Taylor 1979).

COMPOSITION OF THE FAUNA

The composition of the fauna varies from central to southern basins, as well as amongst the different stratigraphic levels.

In the Neuquén Basin, the Lower Cretaceous assemblages are mainly composed by glypheids and mecochirids while the late Cretaceous–early Tertiary one is exclusively composed of callianassids. In the Austral Basin, the Lower Cretaceous fauna is rich and includes several species of erymids, nephropids, and callianassids, while the Senonian forms are poorly known and represented by a few specimens of glypheids, nephropids and callianassids (see text-fig. 6).

In Antarctica, decapod crustaceans are known from late Berriasian to Aptian–Albian deposits in Alexander Island and represent a diversified fauna of callianassids, mecochirids, glypheids, axiids, and erymids (Taylor 1979). They are also known from the late Cretaceous of James Ross and adjacent islands, where an abundant, beautifully preserved fauna of nephropids, callianassids and mecochirids occurs (text-fig. 6).

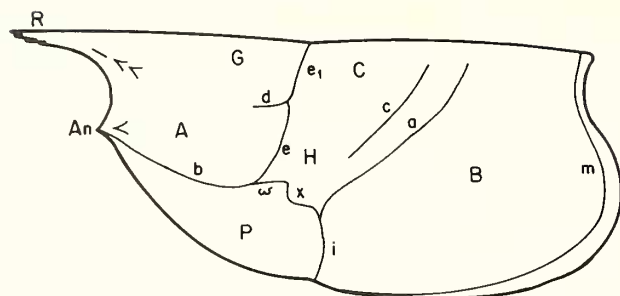
BASIN STAGE	NEUQUEN	AUSTRAL	ANTARCTIC	
			WESTERN	EASTERN
MAASTRICHTIAN	<i>Callianassa burckhardtii</i> <i>Callianassa</i> sp.			<i>Haploparia stokesi</i>
CAMPANIAN		<i>Haploparia antarctica</i>		<i>Callianassa meridionalis</i>
SANTONIAN		<i>Callianassa</i> sp.		<i>Meyeria crafti</i>
CONIACIAN		<i>Glyphea aculata</i>		
TURONIAN		<i>Haploparia arbei</i>		
CENOMANIAN				
ALBIAN				
APTIAN		<i>Palaeastacus sussexiensis</i> <i>Hoploparia</i> sp. A. <i>Enoplaclytia</i> sp. <i>Palaeastacus terraereginae</i>	<i>Enoplaclytia</i> sp. <i>Palaeastacus</i> cff. <i>sussexiensis</i> <i>P. terraereginae</i>	
BARREMIAN		<i>Hoploparia langimana</i> <i>Protocallianassa patagonica</i>	<i>P. faersteri</i> <i>Trachysama</i> aff. <i>ornatum</i>	
HAUTERIVIAN	<i>Glyphea</i> sp. <i>Meyerella rapax</i>	<i>Eryma</i> cff. <i>E. sulcata</i>	<i>Glyphea</i> sp. <i>G. alexandri</i> <i>G. georgensis</i>	
VALANGINIAN	<i>Callianassa</i> aff. <i>peruviana</i>		<i>Mecachirus</i> sp. <i>Schueferia carinata</i> <i>Protacallianassa antarctica</i> <i>P.</i> sp.	
BERRIASIAN	<i>Haploparia</i> sp. B			

TEXT-FIG. 6. Distribution of the Cretaceous decapod crustaceans in the Neuquén, Austral and Antarctic basins.

PRESERVATION

Preservation of fossil decapods is usually good because they mostly occur in concretions. In spite of this, they are only locally common and normally represent a small part of the fossil assemblages which are usually dominated by ammonoids.

Two kinds of concretions are present, calcite concretions or nodules and limonite-cemented sandstone concretions. The calcium carbonate nodules are very 'tight' and hard, and are surrounded by black shales. These nodules were formed during the early stage of diagenesis due to local pH conditions generated by the decomposition of organic matter creating local environments chemically favourable to the formation of calcium carbonate concretions (Waage 1964). The fossils are excellently preserved as one or more fragments at the central core but difficult to prepare because of the toughness of the concretions. Most specimens are articulated and have the carapace filled with calcite-cemented mud. Sandy concretions are found where the fossils are preserved along bedding planes. The concretions are epidiagenetically formed by differential precipitation of iron



TEXT-FIG. 7. Sketch figure of a generalized erymid with the main morphological features of the cephalothorax (modified from Förster 1966).

oxides, which increased the lithification of the sandstone and contributed to the preservation of the fossils.

In some cases (i.e. the Upper Cretaceous callianassids from the Neuquén Basin) the fossils are preserved as partially eroded fragments, loose and dispersed as clasts in a clastic matrix, often associated with trace fossils. Effects of disarticulation or crushing are common, and some specimens are found in moulting position (see Pl. 56, figs. 1–2; Pl. 58, fig. 4).

PREVIOUS OCCURRENCES

The first description of a Cretaceous decapod crustacean from continental Argentina was that of Wilckens (1907), who described and illustrated (a drawing) a specimen of *Hoploparia? antarctica* Wilckens from the late Cretaceous of Southern Patagonia. Böhm (1911) later described palms of *Callianassa burckhardtii* Böhm from the late Maastrichtian–Danian of the Neuquén Basin. In Antarctica, Weller (1903) described and illustrated '*Glyphea*' *stokesi* Weller from the Senonian beds of Snow Hill Island.

A publication hiatus of over fifty years transpired before Ball (1960) described several beautifully preserved specimens of *Hoploparia stokesi* (Weller) from James Ross and adjacent islands, together with remains of *Callianassa meridionalis* and *Meyeria crofti* Ball spp. Del Valle and Rinaldi (1975) subsequently described specimens of *H. stokesi* associated with late Campanian ammonoids from Seymour (Vicecomodoro Marambio) Island.

Taylor (1979) published a comprehensive study of the Lower Cretaceous decapod fauna of Alexander Island, describing and illustrating specimens of *Glyphea alexandri*, *G. georgiensis*, *Schuereria carinata*, *Protocallianassa antarctica*, *Palaeastacus foersteri* Taylor spp., *P. terraereginae* (Etheridge), *P. cf. P. sussexiensis*, *Trachysoma* aff. *T. ornatum*, *Enoplocyrtia* sp. and *Mecochirus* sp.

New specimens from the early Cretaceous of the Austral Basin were studied by Aguirre Urreta and Ramos (1981a), who described: *P. terraereginae* (Etheridge), *Eryma* cf. *sulcata* and *Hoploparia* sp. Aguirre Urreta (1983) described *Protocallianassa patagonica* Aguirre Urreta, *Hoploparia longimana* (Sowerby), *P. terraereginae* (Etheridge) and *Enoplocyrtia* sp. from Barremian deposits of the Austral Basin. A comprehensive summary of the Cretaceous decapod fauna was prepared by Aguirre Urreta (1985b), with the description of glypheids from southern Patagonia and mecochirids from the Neuquén Basin.

Feldmann and Tshudy (1987) published a study on the ultrastructure in cuticles from *Hoploparia stokesi* (Weller) from the López de Bertodano Formation of Seymour Island, Antarctica.

REPOSITORIES

The fossils are deposited in the following institutions.

CIRGEO. Centro de Investigaciones en Recursos Geológicos, Ramírez de Velazco 847. 1414-Buenos Aires, Argentina.

CORD-PZ. Cátedra de Paleontología, Universidad Nacional de Córdoba, Av. Vélez Sarfield 299. 5000-Córdoba, Argentina.
CPBA. Cátedra de Paleontología, Universidad de Buenos Aires, Ciudad Universitaria, Pabellón 2, Geología. 1428-Buenos Aires, Argentina.
MLP. División Paleozoología de Invertebrados, Museo de La Plata, Paseo del Bosque s/n. 1900-La Plata, Argentina.

SYSTEMATIC PALAEOONTOLOGY

Morphological terms are from Förster (1966) and Glaessner (1969). A sketch figure with the most important morphological features present in the cephalothorax of each different family is presented before the respective descriptions (see text-figs. 7, 11, 14, and 17). Localities are numbered as in the text and text-figs. 2, 4 and 5.

Order DECAPODA Latreille, 1803
Suborder PLEOCYEMATA Burkenroad, 1963
Infraorder ASTACIDEA Latreille, 1803
Family ERYMIDAE van Straelen, 1924
Subfamily ERYMINAE van Straelen, 1924
Genus PALAEASTACUS Bell, 1850

Type species. *Astacus sussexiensis* Mantell 1833 (= *Palaeastacus dixonii* Bell 1850) by original designation.

Diagnosis. Erymid with gastroorbital groove weak, postcervical groove strong and separated from branchiocardiac. Chelipeds stout, with square, spiny palm and short fingers.

Comments. There is considerable disagreement between different authors about the taxonomic status of *Eryma* v. Meyer, *Palaeastacus* Bell and *Enoploclytia* McCoy, and the validity of *Phlyctisoma* Bell, as well as their stratigraphic ranges. The erymids were revised by Förster (1966) and a good summary of the discussion is given by Taylor (1979); the former author recognized the four taxa as different genera. *Enoploclytia* and *Palaeastacus* were described as Cretaceous forms, while *Eryma* developed during the Jurassic and became extinct in the early Cretaceous. *Phlyctisoma* is known from Jurassic and Cretaceous localities, but with a more scattered distribution.

Palaeastacus differs from *Eryma* in its more sculptured carapace, in having the postcervical groove stronger than the branchiocardiac and usually subparallel to it, and in having a stout palm with shorter fingers (Förster 1966). The main difference between *Enoploclytia* and *Palaeastacus* are in the form and size of the chelipeds. In the former the chelae are long and slender, with a rectangular palmar portion of the propodus and with long and slender fingers, while in the latter the chelae are stout, with shorter fingers. They also differ in the major or minor development of the postcervical and branchiocardiac grooves (Förster 1966; Glaessner 1969). They were included as two subgenera of *Enoploclytia* by Mertin (1941). *Palaeastacus* differs from *Phlyctisoma* in having a more compressed cephalothorax, weak gastroorbital groove, postcervical groove not joining i and granulose or punctate sculpture, but not as coarse as in the latter genus.

Palaeastacus evolved from *Eryma* in the Jurassic, according to Förster (1966, text-fig. 37). As interpreted here, it ranges from the early Jurassic to the late Cretaceous in different parts of the world, but seems to be more widespread in the early Cretaceous. Different Cretaceous species have been identified in Antarctica (Taylor 1979), Australia (Etheridge 1914; Woods 1957; Hill *et al.* 1968), ?France (Tribolet 1873–4), Great Britain (Bell 1850; Woods 1931), North America (Rathbun 1935; Stenzel 1945; Richardson 1955; Roberts 1962) and Patagonia (Aguirre Urreta and Ramos 1981a; Aguirre Urreta 1983, 1985b; text-figs. 21 and 22).

Palaeastacus sussexiensis (Mantell, 1833)

Text-figs. 8–10

- 1833 *Astacus sussexiensis* Mantell, p. 124, fig. 2.
 1850 *Palaeastacus dixonii* Bell, p. 344, pl. 38, figs. 1–4.
 ?1863 *Hoploparia scabra* Bell, p. 28, pl. 7, figs. 3–7.
 ?1863 *Phlyctisoma granulatum* Bell, p. 36, pl. 11, figs. 9–10.
 1931 *Enoplocyrtia dixonii* (Bell); Woods, p. 83, pl. 23, figs. 9–12; pl. 24, figs. 1–3.
 1941 *Enoplocyrtia (Palaeastacus) sussexiensis* (Mantell); Mertin, p. 161, text-fig. 4a.
 1966 *Palaeastacus sussexiensis* (Mantell); Förster, p. 133, pl. 17, fig. 6.

Material and localities. One specimen corresponding to the left side of the cephalothorax and left first pereopod (CPBA 14097), and a second specimen corresponding to the left side of the cephalothorax and the right manus (CIRGEO 988, F. Medina coll.) from locality 19.

Description. Length of cephalothorax from base of rostrum to posterior margin along mid-dorsal line ranges from 76 to 95 mm.

Anterior region large, ornamented with strong spines arranged in rows near the dorsal margin. A ridge is well defined from the base of rostrum downward and backward. Below this ridge the spines and tubercles are much smaller and more sparsely distributed.

Cervical groove (e–e₁) very deep and well marked, bending anteriorly at mid-side where a shallow depression represents the gastroorbital groove (d). Antennal groove narrow, curving upwards, intersecting the anterior margin near the orbital margin. Postcervical groove (c) well defined, starts near mid-dorsal line and becomes shallow on mid-side. Branchio-cardiac (a) groove better developed, oblique, narrow, starting from mid-dorsal line and joining inferior groove (i). Hepatic groove (b₁) well defined, protuberance x more inflated than w. A marginal groove and carina are well developed in the posterior and ventral margins.

The ornamentation of the cephalothorax is composed of tubercles which are stronger on the dorso-anterior region, becoming smaller on the branchiostegite where they are more densely spaced.

First pereopod large, merus 40 mm long (CPBA 14097), laterally compressed, expanding slightly distally, subtriangular in cross-section; 9–10 spines ornament inner and outer margins, surface covered with small tubercles. Carpus subtriangular, small, with scattered tubercles. Palmar portion of propodus large, oval to circular in cross section. Inner margin ornamented by 7–8 regularly spaced spines; outer side shows smaller scattered spines. Inner surface covered with small tubercles and few big spines, a depression borders the inner margin. Dactylus and pollex at least as long as the palmar portion of the propodus, broken in the two available specimens; at the proximal end circular in cross-section, ornamented with regularly spaced small teeth on the opposite margins.

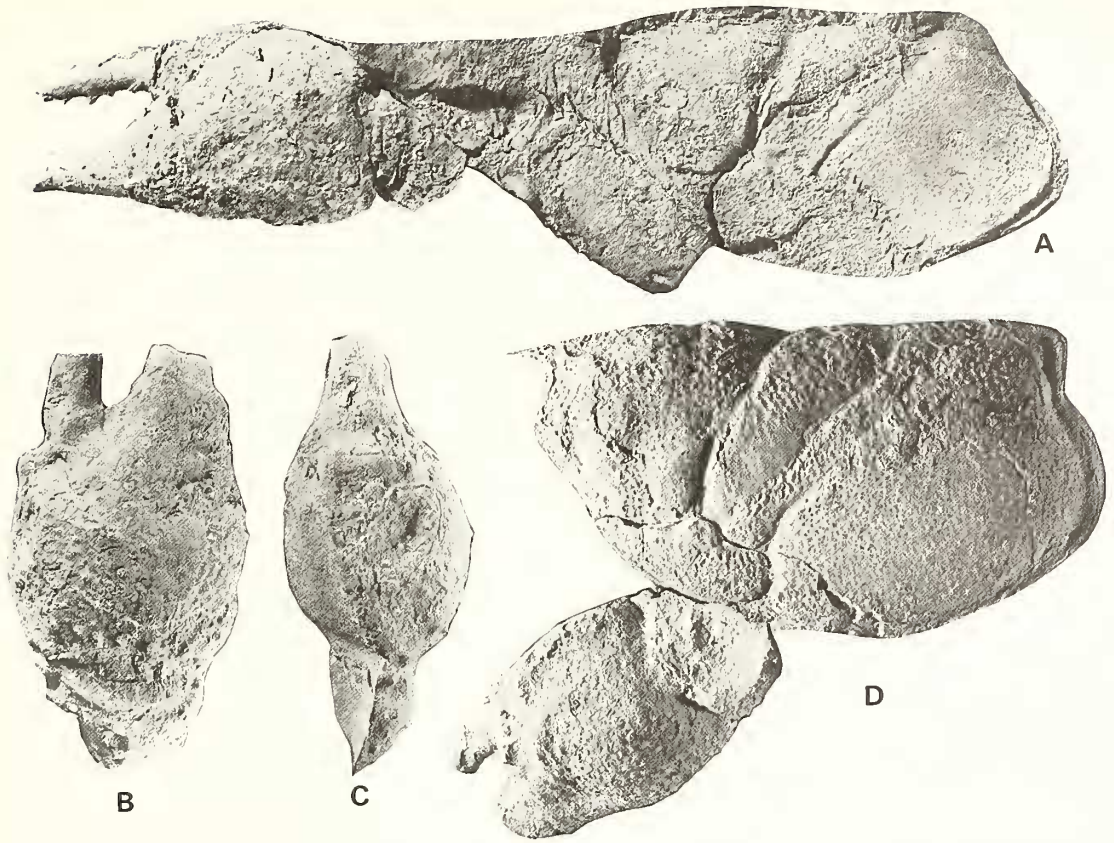
Remarks. The Patagonian material is here assigned to the genus *Palaeastacus* Bell because of the shape and ornamentation of the first pereopod, with stout and square palmar portion of propodus, and the good development of both the postcervical and branchiocardiac grooves.

P. sussexiensis (Mantell) differs from *P. terraereginae* (Etheridge) in its larger size, more elongate cephalothorax with finer ornamentation, different configuration of antennar groove, and less well-marked postcervical groove (Etheridge 1914, p. 273, pl. 23, figs. 1–2; pl. 24, fig. 1; Woods 1957, p. 166, pl. 4, figs. 5–9; text-fig. 6; Aguirre Urreta and Ramos 1981a, p. 606, pl. 1, figs. b–c; pl. 2, figs. a–b; pl. 3, fig. a; text-figs. 3, 4a).

Palaeastacus foersteri Taylor resembles *P. sussexiensis* (Mantell) in having a similar long rostrum and in the possession of a row of spines extending downwards from the base of it. The antarctic species is much smaller, the cephalothorax is more rounded, ornamented with coarse and dense tubercles, and the postcervical and branchiocardiac grooves seem to be partially developed (Taylor 1979, p. 26, pl. 4, figs. b–c; text-figs. 10a–11).

The unique specimen from Antarctica described as *P. cf. sussexiensis* by Taylor (1979, p. 30, pl. 4, figs. d–f; text-fig. 10e) shows an overall resemblance with the Patagonian specimens. Although it is nearly complete, its cardiac region and the chelae are poorly preserved, precluding a proper comparison with the Patagonian material.

Palaeastacus walkeri (Whitfield) compares well with *P. sussexiensis* (Mantell) in its large size and



TEXT-FIG. 8. *Palaeastacus sussexiensis* (Mantell). A, left lateral view of specimen CPBA 14097 showing cephalothorax and left first pereiopod. B–C, lateral and inner view of right manus of D, CIRGEO 988. D, left lateral view of cephalothorax and right manus CIRGEO 988. Locality 19. All figures $\times 0.75$.

stout, strongly ornamented chelipeds, but differs particularly in the lack of branchiocardiac groove (Stenzel 1945).

We agree with Woods (1931, p. 83) in considering *P. scaber* (Bell) synonymous with *P. sussexiensis* (Mantell), although that author accepted the trivial name *dixonii* Bell 1850 not *sussexiensis* (Mantell 1833).

Occurrence. The species is recorded in the upper section of the Río Mayer Formation, *Peltocrioceras deeckeii* Assemblage zone, late Aptian. It was previously known from the Aptian to Lower Cenomanian of England (Woods 1931, p. 85).

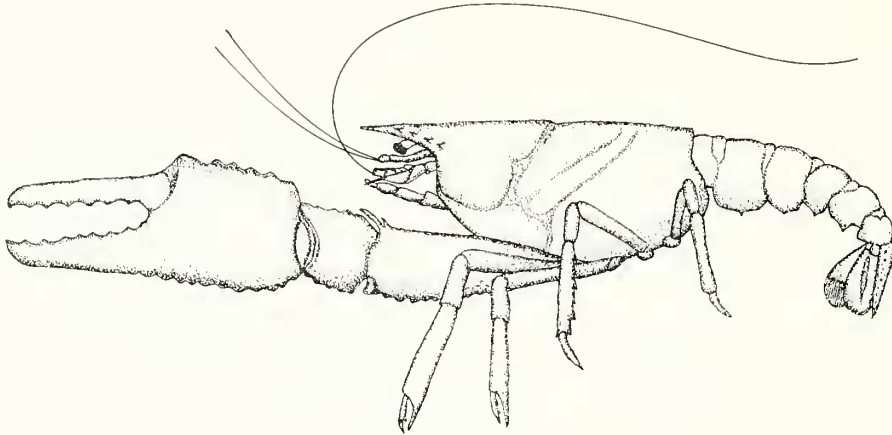
Palaeastacus terraereginae (Etheridge, 1914)

Plate 55, figs. 1–3

- 1914 *Enoploclytia terra-reginae* Etheridge; p. 273, pl. 23, figs. 1–2; pl. 24, fig. 1.
- 1957 *Enoploclytia terrae-reginae* Etheridge; Woods, p. 166, pl. 4, figs. 5–9; text-fig. 6.
- 1968 *Enoploclytia terrae-reginae* Etheridge; Hill *et al.*, pl. k 11, figs. 6–7.
- 1979 *Palaeastacus terraereginae* (Etheridge); Taylor, p. 32, pl. 4, figs. *g–h*; text-fig. 12*a–b*.
- 1981*a* *Palaeastacus terraereginae* (Etheridge); Aguirre Urreta and Ramos, p. 606, pl. 1, figs. *b–c*; pl. 2, figs. *a–b*; pl. 3, fig. *a*; text-figs. 3, 4*a*.



TEXT-FIG. 9. Diagrammatic sketch of cephalothorax of *Palaeastacus sussexiensis* (Mantell) showing the cephalic grooves, $\times 0.67$.



TEXT-FIG. 10. Diagrammatic reconstruction of *Palaeastacus sussexiensis* (Mantell), Approximately $\times 0.33$.

1983 *Palaeastacus terraereginae* (Etheridge); Aguirre Urreta, p. 306, pl. 1, fig. 6; text-fig. 2.

1985b *Palaeastacus terraereginae* (Etheridge); Aguirre Urreta, pl. 2, figs. H-I.

Material and localities. A complete specimen (CPBA 10850) from locality 10; two complete cephalothoraxes, CPBA 10851 and CPBA 11137a from localities 16 and 13, respectively; one fragmentary cephalothorax (CPBA 11671) from the last locality; two complete, crushed specimens and incomplete fragments CPBA 10795, 10839, 10855 and 10856 from locality 12.

Description. Cephalothorax elongate, narrowing somewhat in front, greatest height at mid point; dorsal surface slightly arched, posterior margin sigmoid and ventral margin convex. Rostrum not well preserved. Cervical groove ($e-e_1$) deep, broad, very well defined; slightly sigmoidal at junction with gastroorbital groove (d) that is broad, short, quite deep; lower part bending sharply to join antennal groove (b).

Gastric region ornamented with coarse tubercles; diminishing in size and density towards antennal region. Postcervical groove (c) well marked, beginning a short distance from the mid-dorsal line and extending to the prominence w. Branchiocardiac groove (a) oblique, parallel to c, starting as c and joining inferior groove (i), which is concave in front and reaches the ventral margin anteriorly. Hepatic groove (b_1) distinct; anterior half linking $e-e_1$ with c dorsally to w while the posterior part connects e and a ventrally to x. Depression c_1 distinct. A groove and marginal ridge are present on the posterior margin, both weakening ventrally. Cardiac region coarsely tuberculated, as is the dorsolateral sector of the gastric region. The pterygostomial region and ventral part of the gastric region ornamented with weaker tubercles.

Abdomen with five square segments, sixth segment longer. No detail of the tergites and pleurites visible. Telson partially preserved, shorter than sixth abdominal segment. Entire abdomen seems to be weakly ornamented but the poor preservation precludes any other remark.

First pereopod large, chelate. Merus strong, widening anteriorly with deep furrow on upper side and row of small spines on lower border which continues on triangular carpus. Palmar portion of propodus rounded in section, with subparallel margins, ornamented with sharp tubercles arranged in longitudinal rows; lower

margin with spines. Dactylus and pollex of equal size, subcircular cross section, tapering distally, ornamented with tubercles spread over entire surface. Rest of pereiopods not well preserved.

Remarks. The configuration of the grooves and the ornamentation match well with *Palaeastacus terraereginae* (Etheridge) as described by Etheridge (1914, p. 271, pl. 23, figs. 1–2; pl. 24, fig. 1) and Woods (1957, p. 166, pl. 4, figs. 5–9; text-fig. 6).

P. terraereginae (Etheridge) differs from *Enoploclytia tenuidigitata* Woods, another Australian species, in the arrangement of carapace furrows, shape of chelipeds, and stronger ornamentation (Woods 1957, p. 164, pl. 5, figs. 1–4; text-fig. 6). *Palaeastacus foersteri* Taylor from the ?early Aptian of Antarctica differs from *P. terraereginae* in the slope of the cervical groove and the sigmoid curvature of both postcervical and branchiocardiac grooves together with a stronger tuberculation in the former species (Taylor 1979, p. 26, pl. 4, figs. b–c; text-figs. 10a, 11).

The single specimen of *Palaeastacus* cf. *sussexiensis* described and figured by Taylor (1979, p. 30, pl. 4, figs. d–f; text-fig. 10e) from the ?early Aptian of Antarctica differs from the Patagonian specimens in having a more elongate and narrower cephalothorax, straight cervical groove, absence of gastroorbital groove, stronger ornamentation of abdomen, and marginal groove and carinae restricted to the postero-dorsal part.

The only previously known Lower Cretaceous species from the Northern Hemisphere are, as I interpret the genus, *P. sussexiensis* (Mantell), [= ?*P. scaber* (Bell)], *P. walkeri* (Whitfield) and *P. walkeri schmidtii* (Richardson).

The Patagonian material differs from both subspecies of *P. walkeri* by its smaller and less strongly ornamented first pereiopod, as well as by its better developed postcervical and branchiocardiac grooves, while *P. walkeri walkeri* (Whitfield) lacks the branchiocardiac groove (Stenzel 1945; Richardson 1955). *P. sussexiensis* (Mantell) is larger, with larger chelipeds, smaller tubercles on the cephalothorax, an antennar groove with sharp upward bends terminating on the orbital border, and a row of strong spines extending obliquely downward from base of rostrum (Woods 1931, p. 83, pl. 23, figs. 9–12; pl. 24, figs. 1–3, also see above).

Occurrence. *Palaeastacus terraereginae* (Etheridge) has been reported from the late Albian of Australia (Woods 1957; Hill *et al.* 1968), ?early Aptian of Antarctica (Taylor 1979) and late Barremian–late Aptian of Patagonia (Aguirre Urreta 1983; Aguirre Urreta and Ramos 1981a), where it occurs in the upper levels of the Río Mayer Formation as well as in the Río Belgrano Formation.

Genus ERYMA von Meyer, 1840

Type species. *Macrourites modestiformis* von Schlotheim 1822 by original designation.

Diagnosis. Erymid with subcylindrical cephalothorax, rostrum moderately long, gastroorbital groove weak, cervical groove deep, postcervical and branchiocardiac grooves variably developed, joined or separate, protuberance w distinct, sculpture weak, chelipeds with fingers longer than palm.

Comments. *Eryma* was a widespread genus in the Jurassic that persisted into the early Cretaceous. According to Glaessner (1960, 1969) it is phylogenetically linked with the European Triassic genus *Lissocardia* von Meyer and gave rise to *Palaeastacus* (see also Förster 1966). *Eryma* can be distinguished from *Phlyctisoma* by the shape of cephalothorax, weak gastroorbital groove, more delicate sculpture, and shape and slenderness of chelipeds. *Enoploclytia* differs from *Eryma* in the minor development of the carapace grooves; coarser ornamentation, and slenderness of dactylus and pollex.

As interpreted here, the Cretaceous records of *Eryma* are from Central Europe (van Straelen 1936a), Germany (Harbort 1905; Förster 1966), Great Britain (Woods 1930), ?Lebanon (Roger 1946; Brugnioli Giofredi *et al.* 1975), North America (Rathbun 1923; 1926a and b) and Patagonia (Aguirre Urreta and Ramos 1981a) (see text-figs. 20–21).

Eryma sp. cf. *E. sulcata* Harbort, 1905

Plate 55, fig. 5

1905 *Eryma sulcata* Harbort, p. 15, pl. 1, fig. 11a-b; pl. 11, fig. 4a-c.*Material and locality.* An external mould of cephalothorax and a cheliped (CPBA 10853) from locality 10.*Description.* A single specimen consisting of an external mould of a cephalothorax and a left cheliped is known. The length of the cephalothorax along the mid-dorsal line is 18 mm, excluding the rostrum that is not preserved.

Cervical groove deep, and slightly undulatory, joining the antennal groove below, which curves upward and disappears near antennal spine. Gastroorbital groove weak and very shallow. Postcervical groove deep and narrow, straight and oblique, weakening towards its junction with hepatic groove. Branchiocardiac groove parallel to postcervical, shallower and narrower, joining inferior and hepatic grooves. Protuberances x and w marked.

Ornamentation, as exhibited by the external mould, seems weak, consisting of small rounded tubercles; stronger on dorsal part of the gastric region where the tubercles are less dense and arranged in rows nearly parallel to the dorsal line.

First pereopod chelate, merus partially preserved; carpus small and triangular; palmar portion of propodus subquadrate, inflated, sparsely tuberculated; inner margin with at least nine spines. Pollex and dactylus slender, with circular cross-section; longer than palm, both strongly tapering distally, ornamented with small tubercles.

Remarks. The Patagonian specimen compares well with the specimens figured by Harbort (1905, pl. 1, fig. 11a; pl. 11, fig. 4c) from the early Hauterivian of Germany. However, it differs from other specimens referred to the species (see Woods 1930, p. 80, pl. 22, figs. 5 and 6; Förster 1966, p. 124, pl. 17, figs. 2 and 4; text-fig. 23) in the branchiocardiac groove which is shallow near the dorsal margin, tending to be deeper near its junction with the inferior groove in the Patagonian material. The inverse is true in the European material. The scarcity of the Patagonian material precludes further comparison.*Occurrence.* *Eryma sulcata* Harbort is known from the early Hauterivian of Germany (Harbort 1905; Förster 1966) and the Hauterivian (bed C₄, Speeton) of England (Woods 1930). In Patagonia *E.* cf. *E. sulcata* is associated with *Favrella americana* (Favre) and *Aegocrioceras* sp. of the upper early Hauterivian (Riccardi 1984).

Genus ENOPLOCYTIA M'Coy, 1849

Type species. *Astacus leachi* Mantell, 1822, by original designation.*Diagnosis.* Erymid with long, denticulated rostrum; gastroorbital groove broad, deep and short; postcervical groove joining inferior one, more developed than branchiocardiac; cephalothorax and chelipeds strongly sculptured, dactylus and pollex long, slender and denticulate.

EXPLANATION OF PLATE 55

Figs. 1-3. *Palaeastacus terraereginae* (Etheridge). 1, CPBA 10851 broken along mid-dorsal line, showing left and right views of cephalothorax, locality 16. 2, left lateral view of cephalothorax CPBA 11137a, locality 13. 3, left lateral view of a nearly complete specimen CPBA 10850, locality 10.

Fig. 4. *Enoplocytia* sp. Latex cast of CPBA 10852 showing shape and ornament of left cheliped, locality 15.

Fig. 5. *Eryma* sp. cf. *E. sulcata* Harbort. lateral view of CPBA 10853 showing cephalothorax and left cheliped, locality 10. All figures $\times 1$.



1



2



3



4



5

Comments. Woods (1930) and many other authors considered *Enoploclytia* as a Jurassic–Cretaceous genus, but it should be noted here that Glaessner (1969) indicated that the distinction between Jurassic species of *Eryma* and *Enoploclytia* is uncertain. Förster (1966) restricted the latter genus to the Cretaceous and considered that the first record of *Enoploclytia* is that of *E. tenuidigitata* Woods from the Aptian of Australia, while *Eryma* had become extinct by that time. Only two probable species of *Enoploclytia* seem to be present in Palaeocene and Eocene deposits of North America (Stenzel 1945; Feldmann 1981).

The record of *Enoploclytia porteri* Miller and Ash, as the oldest freshwater decapod crustacean from the Triassic of Arizona (Miller and Ash 1988) is not accepted here. The diminutive, nearly smooth specimen can hardly be placed in *Enoploclytia* (see diagnosis above) or even in the Erymidae. It is probably a true fresh-water crayfish, related to the Northern Hemisphere Astacidae or Cambaridae and allied forms. *Phlyctisoma* differs from *Enoploclytia* by having massive and coarsely sculptured chelipeds.

As understood here, *Enoploclytia* has been recorded from the Cretaceous of Antarctica (Taylor 1979), Australia (Woods 1957; Hill *et al.* 1968), Central and Northern Europe (Schlüter 1862; 1879; Fritsch and Kafka 1887; Glaessner 1932; van Straelen 1936a; Mertin 1941; Förster 1966), Great Britain (Mantell 1833; M'Coy 1849; Woods 1930), Madagascar (Secretan 1964), Niger (Joleaud and Hsu 1935), North America (Rathbun 1935; Stenzel 1945; Beirich and Feldmann 1980) and Patagonia (text-figs. 21 and 22).

Enoploclytia sp.

Plate 55, fig. 4

Material and locality. One external mould of a left cheliped (CPBA 10852) from locality 15.

Description. An external mould of a small left cheliped is preserved. The carpus is incomplete, subtriangular, with surface ornamented with small scattered tubercles. Length of palmar portion of propodus about one and a quarter times its width, ornamentation as in the carpus, a depression runs from the base of dactylus parallel to inner margin. Dactylus and pollex slender, longer than palmar portion of propodus, although their distal ends are not preserved. They are ornamented with small tubercles, inner margins of both regularly toothed, insertion of the dactylus bounded by a rounded collar.

Remarks. The long and slender fingers shown by the specimen allow its inclusion in *Enoploclytia* as I interpret the genus. A cheliped illustrated by Taylor (1979, p. 35, pl. 5, fig. *d*) as ?*Enoploclytia* sp. from the ?early Aptian of Antarctica shows an overall resemblance with the Patagonian specimen, although it is larger. *Enoploclytia leachi* (Mantell), type species of the genus, has thinner and more slender fingers than the Patagonian specimen, as well as stronger tubercles on the surface of carpus and propodus (Mantell 1833, p. 122, fig. 1, Fritsch and Kafka 1887, p. 27, pl. 9, fig. 9; text-figs. 46–52; Woods 1930, p. 85, pl. 24, fig. 4; pl. 25, fig. 1; Mertin 1941, p. 162, pl. 1, figs. 1–8; text-fig. 5).

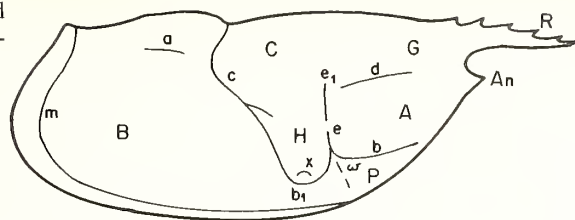
Occurrence. The specimen was found in the lower exposed section of the Río Mayer Formation, associated with ammonites of late early Aptian age (Aguirre Urreta 1985a; Riccardi *et al.* 1987).

Family NEPHROPIDAE Dana, 1852
Subfamily HOMARINAE Huxley, 1879
Genus HOPLOPARIA M'Coy, 1849

Type species. *Astacus longimanus* Sowerby, 1826, by designation of Rathbun (1926b).

Diagnosis. Homarid with long, thin, smooth or denticulate rostrum; cervical groove developed above and below gastroorbital groove; postcervical groove very distinct, connecting with the

TEXT-FIG. 11. Sketch figure of a generalized nephropid with the main morphological features of the cephalothorax (modified from Ball 1960).



cervical groove through semicircular arc; branchiocardiac groove variably developed; chelipeds, long, strong, and generally heterochelous (slightly modified from Glaessner 1969).

Comments. *Hoploparia* is a Cretaceous and early Tertiary genus with a world-wide distribution, but with questionable validity. Pelseneer (1886) indicated that the only difference between *Hoploparia* and *Homarus* was in the rostrum, which was not serrated in the former genus. Woods (1930) compared the fossil material with living species of *Homarus* and decided that they were synonymous, adding that in well-preserved fossil specimens of *Hoploparia* the rostrum was dentated. Van Straelen (1936b) also considered it to be a junior synonym of *Homarus*. Beurlen and Glaessner (1930) indicated that *Homarus* was derived in the Tertiary from a Cretaceous species of *Hoploparia*, while Mertin (1941) extended the range of the latter genus to the early Tertiary, which then gave rise to *Homarus*.

According to Woods (1957) there is a close phylogenetic relationship between both genera, but there are also enough morphological differences to retain them as valid genera. *Hoploparia* has a more granulated carapace, greater development of cephalic grooves, development of an antennar ridge, relatively larger abdominal pleura, thinner chelipeds, and longer and less spinous rostrum (Woods 1957, p. 168). Although Glaessner (1969) maintained both as valid genera, he noted that the distinction between some species is difficult and disputed. Taking into account the previous reasons, I consider that *Hoploparia* and *Homarus* should be retained as different genera, one mostly restricted to the Cretaceous, while the other developed since early Tertiary times. Feldmann (1974, p. 591) observed that *Hoploparia* was probably ancestral to *Homarus* and *Nephrops* Leach. Recently Quayle (1987) described representatives of both *Homarus* and *Hoploparia* from English Eocene deposits and, although not clearly stated, it seems that he maintained both *Homarus* (Cretaceous–Recent) and *Hoploparia* (Lower Cretaceous–Middle Eocene) as valid genera.

Species here referred to *Hoploparia* have been recorded from Cretaceous beds of Antarctica (Weller 1903; Ball 1960; del Valle and Rinaldi 1975, Feldmann 1984, Feldmann and Tshudy 1987), Australia (Etheridge 1917; Woods 1957; Hill *et al.* 1968), North-Central Europe (Roemer 1840; Schlüter 1862; 1879; Harbort 1905; Stolley 1924; van Straelen 1936b; Mertin 1941), France (Robineau-Desvoidy 1849; Tribolet 1873–4; 1874–5), Great Britain (Sowerby 1826; M'Coy 1849; 1854; Bell 1863; Woods 1930; 1931), ?Lebanon (Glaessner 1945; Brugnioli Giofredi *et al.* 1975), Madagascar (Secretan 1964), North America (Pilsbry 1901; Rathbun 1926a, b; 1935; Stenzel 1945; Roberts 1962; Feldmann 1974; Feldmann *et al.* 1977, Bishop 1983a; 1985), Soviet Union (Crimea (Caucasus), Borrisjak 1904), Sweden (Schlüter 1874) and Patagonia (Aguirre Urreta 1983; 1985b) (see text-figs. 21–22).

Hoploparia arbei sp. nov.

Plate 56, figs. 1–8, text-figs. 12 and 13

1985b *Hoploparia antarctica* Wilckens; Aguirre Urreta, pl. 2, fig. A.

Diagnosis. *Hoploparia* with very well developed cephalic grooves, including a, with tuberculated ridge above this groove, cephalic cross-section lanceolate, abdominal pleura with two tubercles, one

in anterior part, located on boundary between tergum and pleuron, and the other on the ventral point.

Holotype. A specimen with well preserved cephalothorax, abdomen and tail fan, and fragmentary pereopods (CPBA 14564), from locality 20 (A. Riccardi, H. Klinger and B. Aguirre Urreta coll.).

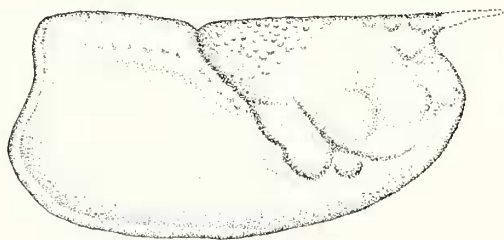
Etymology. Named after Hugo Arbe who collected the first specimens of this species.

Material and localities. The holotype and more than thirty pieces comprising eight specimens corresponding to cephalothoraces and abdomens with tail fan (MLP 21573–21576, CPBA 14565–14568), ten cephalothoraces (MLP 21577–21581, CPBA 14569–14573), 19 abdomens (MLP 21582–21591, CPBA 14574–14582), three fragmentary chelipeds (MLP 21592, CPBA 14583–14584) (A. Riccardi, H. Klinger and B. Aguirre Urreta coll.), and a specimen (MLP 16102) (H. Arbe coll.) corresponding to a fragmentary abdomen with part of cheliped from the type locality.

Description. Medium to large sized, cephalothorax subcylindrical to suboval ($L/W = 2.14\text{--}2.36$, $L/H = 1.80\text{--}2.10$) tapering both anteriorly and posteriorly, rostrum not well preserved in any specimen. Anterior region large, 55–65 % of total cephalothoracic length measured along mid-dorsal line (from base of rostrum to posterior end). Maximum height is nearly at the middle of cephalothorax; greatest width on mid-posterior part of the branchiostegite.

Postcervical groove (c) very well defined, deep and broad, obliquely extending downward and forward, curving and becoming shallower to meet dorsal end of cervical groove ($e\text{--}e_1$); cervical groove well developed, deep and narrow, extending ventrally to merge into the antennar groove (b); hepatic groove (b_1) deep and broad, connecting c and $e\text{--}e_1$; bordering ventrally a very well developed 'adductor testis' region x. Protuberance w prominent and granulose. Branchiocardiac groove (a) weak, bordered dorsally by a tuberculated ridge extending downwards parallel to postcervical groove.

Anterior region quite smooth, with granules on dorsum. A pair of ridges extends on the dorsal surface up nearly to middle of the region; a postorbital spine well developed and three large spines dorsal to the antennar groove, located from the anterior margin up to cervical groove (see text-fig. 12). In the area delimited by $e\text{--}e_1$ and $b_1\text{--}c$, there are small granules, more prominent over x and w. These granules are also noticeable on the dorsal part of the branchiostegite, which is evenly covered by small and rounded pits.

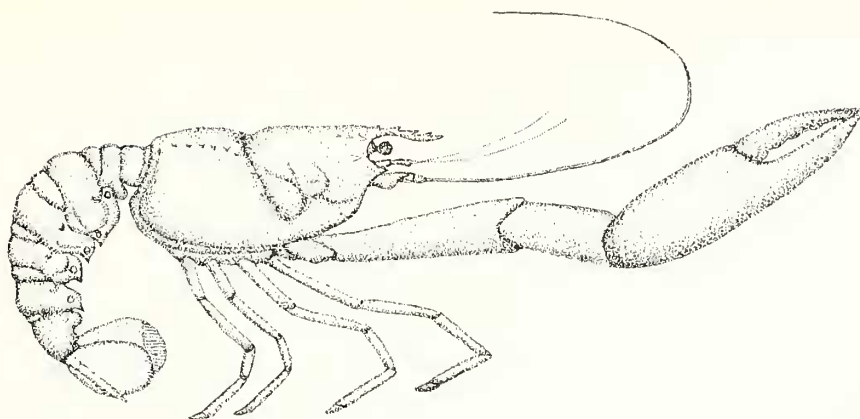


TEXT-FIG. 12. Diagrammatic sketch of the cephalothorax of *Hoploparia arbei* sp. nov. showing the cephalic grooves, $\times 0.67$.

Eyes are preserved in two specimens (see Plate 56, fig. 2, arrowed); the orbits are small, well defined, bounded by narrow ridge. Basal articulation of antennae and parts of third maxilliped also preserved in some specimens (see Plate 56, fig. 3).

Abdomen completely covered by small pits. First segment small, with reduced pleuron; second segment the largest, third to fifth decreasing progressively in size, but all heart-shaped; sixth subtrapezoidal. Each segment has prominent articulating furrows, continuing anteriorly and posteriorly onto pleura, not forming a complete rim. Two tubercles present in each segment: one in anterior part, located on the boundary between tergum and pleuron, another on ventral point, which has a spine directed backwards. Uropods large, smooth, exopod with diaresis, telson subrectangular, with longitudinal ridges and furrows, pitted as abdominal segments.

First pereopod incomplete, strong, large. Merus long, widening distally, with a spine at point of articulation with carpus, which is stout and subquadrate, both ornamented with scattered granules and the carpus also with two rows of tubercles on outer border. Palmar part of propodus at least as long as merus, longer than wide, with oval cross-section, outer margin with two rows of four tubercles each, inner margin with a carina bounded by a furrow that continues on fixed finger. Dactylus not preserved. Other walking legs poorly preserved but very much smaller in comparison with first chelipeds (text-fig. 13).



TEXT-FIG. 13. Diagrammatic reconstruction of *Hoploparia arbei* sp. nov., $\times 0.67$.

Remarks. After examining more than sixty species of *Hoploparia*, only five show a similar pattern of grooves in the cephalothorax to *H. arbei* sp. nov. I will only compare the new species with them and with those Cretaceous species known from nearby.

H. longimana (Sowerby) can be distinguished from *H. arbei* sp. nov. by its comparatively larger chelipeds, smooth cephalothorax, especially on anterior part, and absence of branchiocardiac groove and ridge (Sowerby 1826, p. 493, pl. 18; Woods 1931, p. 90, pl. 25, fig. 5, pl. 26, figs. 2–4).

H. bearpawensis Feldmann can be separated from *H. arbei* sp. nov. by the prominent spinose keel on mid-line, the single spine ending the ridge posterior to c, the abdominal terga with coarsely reticulate, raised, triangular area on the posterior edge of the tergum and triangular pleura (Feldmann *et al.* 1977, p. 1176, pl. 3, figs. 1–6).

H. pusilla Secretan can be distinguished from *H. arbei* sp. nov. by its subquadrate cephalothorax, smooth anterior region, nearly straight postcervical groove, absence of branchiocardiac groove and different shape of abdominal pleura (Secretan 1964, p. 109, pl. 10, figs. 3–4).

H. pelseneeri van Straelen differs from *H. arbei* sp. nov. by the absence of ridge posterior to c, nearly smooth carapace and poorly developed post-orbital spine (van Straelen 1936a, p. 18, pl. 3, figs. 2–3).

At first sight the species that most resembles *H. arbei* sp. nov. is *H. biserialis* Fritsch from the Turonian of Bohemia (see Fritsch and Kafka 1887, p. 35–36, pl. 3, fig. 5, pl. 5, figs. 1–3, text-fig. 56). However, Mertin (1941) considered that the isolated chelipeds probably belong to *H. longimana*, while the rest of the material should be included in the genus *Oncopareia* Bosquet.

H. stokesi (Weller) also presents a similar pattern of cephalic grooves but it is a strongly spinose species, with the abdomen ornamented with well developed tubercles on terga and pleura. Chelipeds of this species are also strongly ornamented and show articular processes between the propodus and dactylus (Ball 1960, p. 10, pl. 1, fig. 4a; text-fig. 2; del Valle and Rinaldi 1975, p. 4, figs. 2–9, also see below and pl. 58, figs. 3, 5–7).

H. arbei sp. nov. can be separated from the incompletely known *H. antarctica* by the absence of a rim in the abdominal pleura and the presence of a tubercle at the end of each one.

Occurrence. The species occurs in the Puesto El Alamo Formation of Southern Patagonia associated with ammonoids indicating the Turonian–Coniacian boundary.

Hoploparia longimana (Sowerby, 1826)

Plate 57, figs. 1–3

- 1826 *Astacus longimanus* Sowerby, p. 493, pl. 18.
 1854 *Hoploparia saxbyi* McCoy, p. 116, pl. 4, fig. 1.
 1863 *Hoploparia longimana* (Sowerby); Bell, p. 26, pl. 6, figs. 1–3.
 1863 *Hoploparia punctulata* Bell, p. 27, pl. 5, figs. 11–13.
 1863 *Hoploparia granulosa* Bell, p. 27, pl. 7, figs. 1–2.
 1863 *Hoploparia sulcirostris* Bell, p. 25, pl. 5, figs. 8–10.
 1931 *Hoploparia longimana* (Sowerby); Woods, p. 90, pl. 25, fig. 5, pl. 26, figs. 2–4.
 1983 *Hoploparia longimana* (Sowerby); Aguirre Urreta, p. 308, pl. 1, figs. a, b, d, text-fig. 3.
 1983 *Enoplocyrtia* sp. Aguirre Urreta, p. 307, pl. 1, fig. c.
 1985b *Hoploparia longimana* (Sowerby); Aguirre Urreta, pl. 2, figs. E–F.
 1985b *Enoplocyrtia* sp. Aguirre Urreta, pl. 2, fig. K.

Material and localities. One abdomen (CPBA 11136), one right (CPBA 11135), and part of a left cheliped (CPBA 11134) from locality 13.

Description. Second to sixth abdominal segments preserved, the first incomplete and the tail fan missing. Specimen of medium size (50 mm), transverse section convex. Every tergum shows an anterior transverse groove which curves to the postero-ventral border and becomes feeble on pleuron. Anterior margin of each segment partially covered by the posterior border of the subsequent one, forming the articulations. Every segment presents a transverse posterior furrow, less marked than the anterior. This posterior furrow curves forwards and downwards upon reaching the pleuron.

Pleuron of second segment round, partially covering third pleuron. Pleura 3 to 5, subtriangular, with posterior border rounded, ending acutely in a small spine directed backwards. Sixth segment trapezoidal, a curved furrow runs parallel to the ventral margin. Coxa and basis of left uropod partially preserved. Although the specimen is slightly eroded, the ornamentation seems to be weak, and shows small pits, scattered on the terga and more densely spaced on pleura.

Two partially preserved chelipeds available, the right one shows the distal part of propodus and fingers, the left one only fingers. The palmar part of the right propodus has a planar upper surface and convex lower surface. External margin bounded by a furrow which extends onto fixed finger, internal border with a line of coarse spines. Surface covered with very few tubercles of irregular size. Fingers 55 mm long. Dactylus straight, distal end curves inward facing the end of pollex, which is gently curved. Fingers ornamented with small, evenly spaced granules; opposite margins with few rounded teeth of variable size. Fingers of left cheliped 50 mm long. Pollex straight, tapering distally, with oval cross section, tip bending inwards, dactylus curved to pollex, opposite borders with fine, small and numerous teeth. Surface nearly smooth, with scattered small tubercles; spines are preserved on outer margin of dactylus.

Remarks. The Patagonian material compares well with that described and illustrated by Woods (1931, p. 90, pl. 25, fig. 5; pl. 26, figs. 2–4). The original diagnosis of the species mostly refers to chelipeds (Sowerby 1826, p. 493, pl. 18), which are very similar to those described here. The original drawings show, however, slight differences such as the more regular disposition of the teeth in the opposite margins of the fingers of right chelae (see *Hoploparia* sp. A below), and the presence of a

EXPLANATION OF PLATE 56

Hoploparia arbei sp. nov. 1, lateral view of holotype CPBA 14564 showing cephalothorax, abdomen, part of the tail fan and broken pereopods. 2, lateral view of MLP 21573 showing cephalothorax and abdomen, the right eye is arrowed. 3, lateral view of CPBA 14569 showing cephalothorax, basal segments of antenna and part of left merus and carpus. 4, lateral view of MLP 16102 showing a fragmentary abdomen with part of cheliped. 5, lateral view of CPBA 14565 with very well preserved cephalothorax, part of abdomen and right merus. 6a–b, outer and lateral views of CPBA 14583 showing carina and part of fixed finger. 7, lateral view of MLP 21582 showing abdomen, tail fan and broken pereopod locality 20. All figures $\times 1$. Figure 3 lit from bottom right.



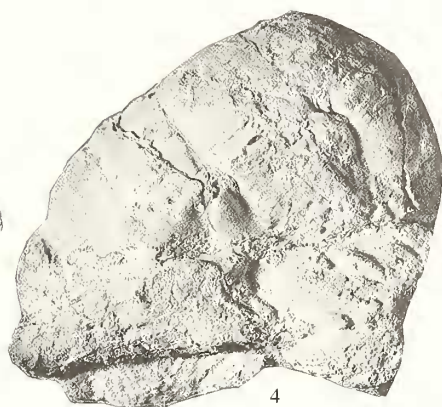
1



2



3



4



5



6a



6b



7

marked rim in the pleuron of second abdominal segment. This feature is not present in the material illustrated by Woods (1931), who also stated that the type cannot be found.

I agree with Woods (1931) in considering *H. saxbyi* M'Coy, *H. punctulata*, *H. sulcirostris* and *H. granulosa* Bell spp. as junior synonyms of *H. longimana* (Sowerby). *H. mesembria* Etheridge, from the late Albian of Australia, differs from *H. longimana* (Sowerby) in having a densely punctate abdomen and heart-shaped second abdominal pleuron with wide outer rim. Both species are also separated by the different configuration of grooves and the relative proportions of carapace, abdomen and first chelipeds (Woods 1957, p. 171, pl. 6, figs. 1-4; text-fig. 7; Hill *et al.* 1968, pl. k 11, fig. 3).

H. longimana (Sowerby) differs from *H. antarctica* Wilckens, known only from three partially preserved abdomens of the Upper Cretaceous of Southern Patagonia, in weak development of the anterior transverse groove, lack of ornamentation, and absence of the posterior transverse furrow and outer rim (Wilckens 1907, p. 108, pl. 3, fig. 5, see also below and Pl. 57, figs. 4a-b).

H. stokesi (Weller) from the late Cretaceous of Antarctica is a strongly spinose species, with the abdomen ornamented with well developed tubercles and all the pleura ending in acute spines. Chelipeds of this species are also strongly ornamented and show articular processes between the propodus and dactylus (Ball 1960, p. 10, pl. 1, fig. 4a; text-fig. 2; del Valle and Rinaldi 1975, p. 4, figs. 2-9, also see below and plate 4, figs. 3, 5-7).

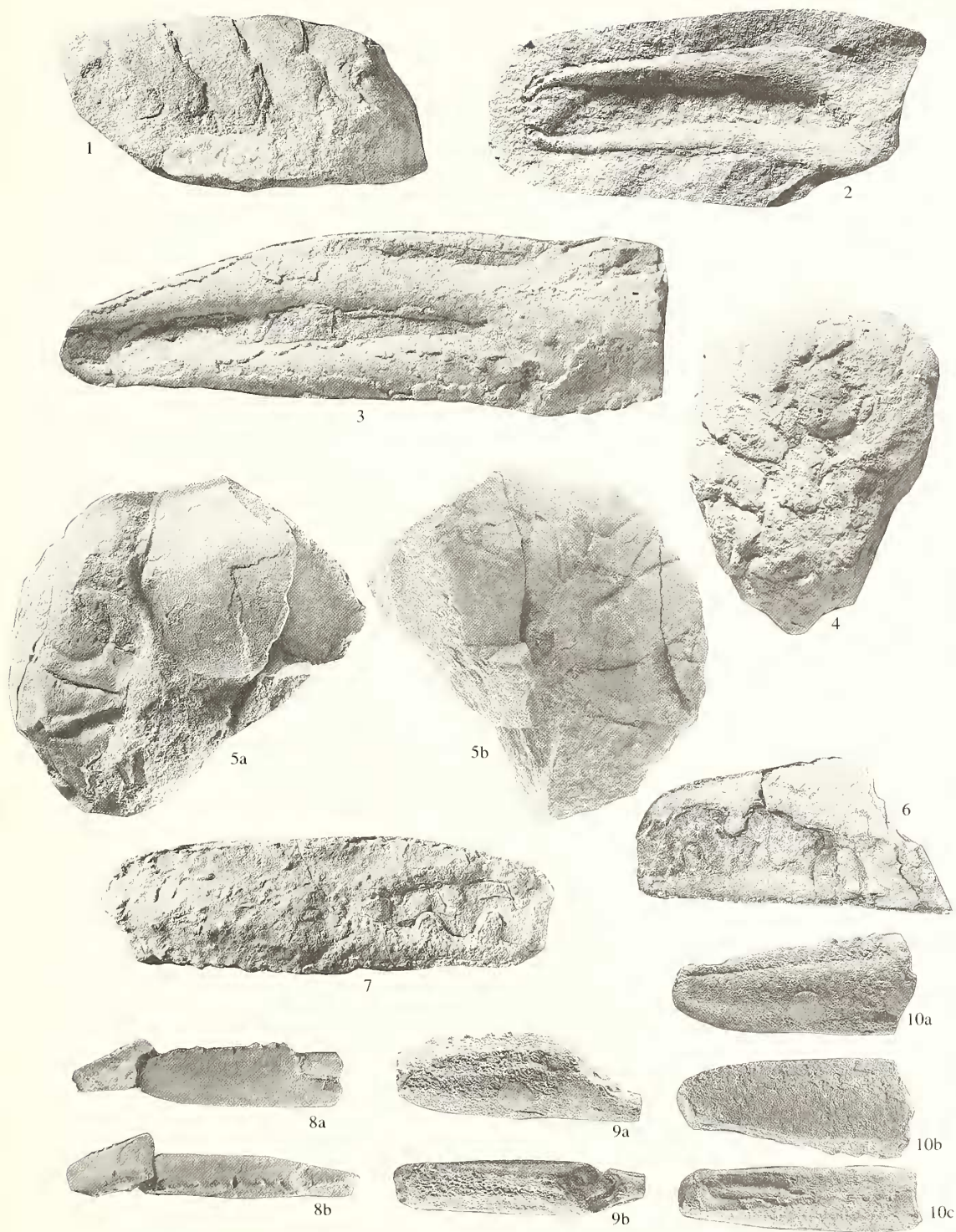
H. collignoni (van Straelen), an Albian species from Madagascar, differs from *H. longimana* (Sowerby) in the evenly punctate ornamentation of the abdomen, the different shape of second pleuron which also shows a well marked outer rim, and the long, narrow first propodus, with dense, rounded tubercles (Secretan, 1964, p. 98, pl. 6, fig. 1; pl. 8, figs. 2-3; pl. 9, figs. 5-10; pl. 10, fig. 1). *H. intermedia* Secretan is known from cephalothoraces and appendages alone, and no abdomens are preserved. The species differs from *H. longimana* in its smaller size, the different configuration of the cephalic grooves and the relative size of the propodus which is short, oval with internal and external margins with strongly developed spines (Secretan 1964, p. 102, pl. 4, figs. 6-10; pl. 9, fig. 11).

H. sculpta Secretan, is easily separated from *H. longimana* (Sowerby) in the strong ornamentation of the dorsal part of the terga as well as the tubercles present in the anterior boundary between terga and pleura. Another difference occurs in the propodus, which is long, narrow, and ornamented with 3 or 4 rounded spines on the internal border of the Madagascan species (Secretan 1964, p. 105, pl. 6, fig. 11; pl. 9, figs. 1-4, 12; pl. 10, figs. 2, 5-9).

Occurrence. *H. longimana* (Sowerby) is known from the Aptian to Lower Cenomanian of England (Woods 1931). Van Straelen (1936b) referred material to this species from several localities in France, but as no illustrations were given, the assignment cannot be confirmed. The species also occurs in the Río Mayer Formation of Patagonia associated with ammonoids of the late Barremian.

EXPLANATION OF PLATE 57

- Figs. 1-3. *Hoploparia longimana* (Sowerby). 1, left lateral view of abdomen, CPBA 11136. 2-3, lateral views of left CPBA 11134 and right chelipeds CPBA 11135, locality 13.
- Figs. 4-5. *Hoploparia antarctica* Wilckens. 4, holotype MLP 4213 showing nearly complete abdomen and part of the tail fan, locality 23. 5a-b, two lateral views of part of branchiostegite and abdomen CORD-PZ s/n 24.
- Figs. 6-7. *Hoploparia* sp. A. 6, lateral view of fragmentary chelae CPBA 10858a, locality 18. 7, lateral view of right manus CPBA 10857, locality 17.
- Figs. 8-10. *Hoploparia* sp. B. 8a-b, lateral and upper views of left cheliped MLP 306a. 9a-b, the same views for specimen MLP 306b. 10a-c, lateral and upper views of right propodus MLP 306c, locality 5. All figures $\times 1$.



Hoploparia antarctica Wilckens, 1907

Plate 57, figs. 4 and 5

1907 ?*Hoploparia antarctica* Wilckens, 1907, p. 12, pl. 3, fig. 5.1985b *Hoploparia antarctica* Wilckens; Aguirre Urreta, pl. 1, fig. H; non pl. 2, fig. A.

Material and localities. The holotype, an abdomen with partially preserved tail fan (MLP 4213, R. Hauthal coll.) from locality 23, and another specimen (CORD-PZ s/n) corresponding to the abdomen and posterior part of cephalothorax from locality 24 (M. Hünicken coll.).

Description. Posterior portion of branchiostegite preserved, showing the end of a ridge that extends upward on each flank, nearly parallel to the dorsal line that accompanies the branchiocardiac groove. Due to this ridge, the cross-section of the cephalothorax at this point is subpolygonal. Ornamentation is almost absent, only small granules and pits are present. A strong and well marked marginal groove and rim are present, at least postero-dorsally.

The abdomen seems to be generally smooth, the only ornamentation consisting of very small, rounded, blunt tubercles and tiny granules scattered on the surface of the terga. Terga of first to fifth somites arcuate, with an anterior furrow separating the articulating element from the external one. Posteriorly terga bounded by a less marked furrow.

Pleura smooth; pleuron of first somite not preserved, that of second large, heart-shaped, ending with a spine on the postero-ventral corner. Pleura of third to fifth somites subtriangular, ending in a small spine directed backwards. Surface of each pleuron has an extension of the anterior groove of the terga that curves downwards and backwards. This groove meets another one that bounds the posterior margin. Thus, the pleuron shows an inner central part bounded by a broad outer rim (plate 57, figs. 5a–b). Sixth somite subtrapezoidal, the tergum is separated from the pleuron by a shallow and broad groove. Pleuron small, smooth, triangular.

Right uropod incomplete, coxa and basis fused, endopod with well developed medial ridge, exopod not preserved. Telson incomplete, subquadrate, with straight lateral margins, posterior margin not preserved.

Remarks. To the author's knowledge the species that most resembles *H. antarctica* Wilckens is *H. brittonestrus* (Stenzel) from the Turonian of Texas. This has a ridge adjacent to the branchiocardiac groove on the postero-dorsal part of the branchiostegite, a marginal groove and raised rim and the overall shape and ornamentation of the abdomen are similar (Stenzel 1945, p. 425, pl. 40, figs. 1–7; text-fig. 11). The only apparent differences seem to be the weaker outer rim present in the pleura of *H. brittonestrus* (Stenzel), the absence of a tubercle in the anterior boundary between terga and pleura and the overall smaller size.

H. bearpawensis Feldmann (Feldmann *et al.* 1977, p. 1176, pl. 3, figs. 1–6) has a prominent spinose keel on midline which is absent in *H. antarctica* Wilckens and the abdomen of the former species has a raised, coarsely reticulated triangular area on the terga. All the somites are of similar size.

The abdomen of *H. tennesseensis* Rathbun from the late Cretaceous of the United States differs from that of *H. antarctica* Wilckens in the rounded outline of the pleura, stronger submarginal groove and more dense ornamentation (Rathbun 1926a, p. 186, pl. 64, figs. 1–9; pl. 65, figs. 1, 3, 6).

The shape of the segments of the abdomen of *H. sculpta* Secretan is similar to that of *H. antarctica*, but the former has stronger tubercles, especially on the dorsal part of the terga (Secretan 1964, p. 105, pl. 10, figs. 6–9). In contrast, the ornamentation of *H. collignoni* (van Straelen) resembles that of the Patagonian species, but differences are noticeable in the shape and outline of the pleura, especially that of the second segment (Secretan 1964, p. 98, pl. 9, fig. 10).

H. stokesi (Weller) from the late Senonian of Antarctica differs from *H. antarctica* in lacking an outer rim on the pleura and in having scattered big tubercles on the terga (Ball 1960; see also below).

H. mesembria Etheridge from the Late Albian of Australia also shows a feeble carina bounding the branchiocardiac groove laterally and the abdomen resembles that of *H. antarctica* Wilckens. However, the Australian species has a proportionally larger abdomen when compared with the

cephalothorax, the ornamentation is more dense, the pleura terminate in a stronger spine and the second segment shows a broader outer rim (Woods 1957, p. 169, pl. 6, figs. 1–4; text-fig. 7).

Occurrence. The species occurs in the Cerro Cazador Formation (Campanian-Maastrichtian) of Southern Patagonia.

Hoploparia stokesi (Weller, 1903)

Plate 58, figs. 1–7

- 1903 *Glypheia stokesi* Weller, p. 418, pl. 1, fig. 1.
- 1960 *Hoploparia stokesi* (Weller); Ball, p. 6, pl. 1, figs. 1–5; pl. 3, figs. 1–2; text-figs 2, 3A.
- 1975 *Hoploparia stokesi* (Weller); del Valle and Rinaldi, p. 4, figs. 2–9.
- 1984 *Hoploparia stokesi*; Feldmann, fig. 2A.

Material and localities. One partially preserved cephalothorax with both chelipeds (CIRGEO 1020, R. del Valle and C. Rinaldi coll.), three cephalothoraces (CIRGEO 983–985); one left cheliped (CPBA 14120); three specimens consisting of cephalothoraces, abdomens, tail fans and broken pereopods (CIRGEO 979–981); one abdomen and tail fan (CIRGEO 982) and several fragmentary specimens from undetermined localities on Seymour (Vicecomodoro Marambio) Island (F. Medina coll.). One fragmentary left cheliped and an external impression of left cheliped (CIRGEO 986–987) from locality 30 (F. Medina and R. del Valle coll.).

Description. Small to medium-sized, cephalothorax suboval, tapering both anteriorly and posteriorly. Rostrum long, serrated. Anterior region large, about 50 to 65% of total length of the cephalothorax measured along mid-dorsal line; greatest width two thirds of the length from base of rostrum; maximum height is at the middle of the cephalothorax. Two ridges on the anterior region extending from base of rostrum onto the dorsal surface are directed backwards and downwards. Post-orbital spines not well preserved in most of available specimens.

A prominent isolated spine occurs near middle of anterior region, above the cervical groove which is well developed on its lower part only, joining a strongly marked antennar groove (b) which curves upwards and becomes shallower towards the anterior margin. Hepatic groove (b₁) deep, very well defined, joining postcervical (c) and cervical (e–e₁) grooves. Protuberance w well marked, dorsally bounded by antennar groove and posteriorly by hepatic groove. Postcervical groove broad, deep, crossing dorsal mid-line nearly perpendicular to it, bending sharply downwards and forwards on the side to meet hepatic groove well down the flank. A rounded ridge present posterior to post-cervical groove. Branchiocardiac groove indistinct and gastroorbital hardly visible on most of available specimens. A shallow short groove extends from postcervical at mid-flank, not reaching the cervical. Marginal groove and rim well developed especially on the postcro-dorsal margin.

Ornamentation consists of spines and granules directed forward, coarse on dorso-anterior surface, decreasing in size on branchiostegite, but densely and evenly spaced there. This feature can be seen when the specimens have the cuticle preserved. If not, the ornamentation looks much finer. The abdominal segments and parts of the tail fan are preserved.

The first segment is short, square, with well developed posterior furrow, pleuron not preserved. Second segment largest, with anterior and posterior transverse grooves, the latter extending on the pleuron. Tergum shows some big scattered tubercles and a prominent, rounded tubercle divides the tergum and pleuron. Both bear dense, small, rounded pits. Pleuron large and rounded, ending in a backward directed spine. Terga of third to fifth abdominal segments are like the former, but smaller. Pleuron with anterior margin rounded, tip with spine. Sixth segment subquadrate, ornamented as the others. Uropods not well preserved. Telson slightly longer than wide, with subparallel margins, ornamentation not clearly seen on material, although it looks like that on the abdominal somites.

Chelipeds long, stout, spinous, heterochelous, much longer than cephalothorax. Merus long, narrow, with rounded section, ornamented with spines that cover all the surface. Carpus half the length of the merus, also with circular cross-section, with large and acute spines directed anteriorly. Palmar portion or left cheliped longer than wide, widening distally; cross-section oval; external surface flat, covered with rounded tubercles; inner margin with a carina bounded by a furrow that continues on fixed finger; outer margin with a row of at least six spines. Internal surface convex, with small tubercles. Articular processes present on the articulation of propodus and dactylus. Both fingers as long as propodus, of equal size. Dactylus straight, pollex slightly

incurved, ornamented with evenly spaced, rounded tubercles; opposite margins with very small, irregular teeth. Right cheliped similar to left, but with longer and more slender fingers. Rest of pereopods partially preserved, but very much thinner and more slender than first pair.

Remarks. This species has been previously described by Ball (1960), but the comparisons are not fully complete. Recently, Feldmann and Tshudy (1987) showed that cuticular ultrastructure may be used to distinguish molted remains and corpses in nephropids, utilizing a large collection of *H. stokesi* (Weller).

H. stokesi (Weller) can be separated from *H. longimana* (Sowerby) by its coarser ornamentation, more spinous abdominal pleura, longer chelipeds with smaller and less differentiated teeth on opposite margins. The Antarctic species can also be differentiated from *H. antarctica* Wilckens by its coarser abdominal ornamentation and lack of an outer pleural rim.

H. collignoni (van Straelen) differs from *H. stokesi* (Weller) in the different pattern of the cephalic grooves, smooth abdomen with rounded pleura and smaller and less ornamented chelae (Secretan 1964, p. 98, pl. 6, fig. 1; pl. 8, figs. 2–3; pl. 9, figs. 5–10; pl. 10, fig. 1). *H. intermedia* and *H. sculpta* Secretan spp. (1964, p. 102, pl. 4, figs. 6–10; pl. 9, fig. 11; p. 105, pl. 4, fig. 11; pl. 9, figs. 1–4, 12; pl. 10, figs. 2, 5–9) have a less ornamented cephalothorax, different pattern of cephalic grooves and smaller pereopods.

The cephalic grooves of *H. pusilla* Secretan, from the Campanian of Madagascar show a general resemblance to those of *H. stokesi* (Weller). The two species can be separated by the different shape of the abdominal pleura, and, according to Secretan (1964, p. 109, pl. 10, figs. 3–4), the branchiocardiac groove is absent in *H. pusilla*, while slightly visible in *H. stokesi* (Weller). *H. mesembria* Etheridge is distinguishable by its finer ornamentation, and the different proportions of cephalothorax, abdomen and first pair of pereopods (Woods 1957, p. 169, pl. 6, figs. 1–4; text-fig. 7).

H. bearpawensis Feldmann shows a prominent spinose keel on midline that makes it easily distinguishable from *H. stokesi* (Weller) (Feldmann *et al.* 1977, p. 1176, pl. 3, figs. 1–6). *H. mickelsoni* Bishop, from the Lower Campanian of North America can be separated from *H. stokesi* by its discontinuous cephalic grooves, anterior cephalic ridges, shape of the second pleuron and general lack of tubercles (Bishop 1985, p. 609, figs. 3.1, 4–5, table 2).

Occurrence. The species is known from several localities of Campanian–Maastrichtian age of the eastern basin of the Antarctic Peninsula.

Hoploparia sp. A

Plate 57, figs. 6 and 7

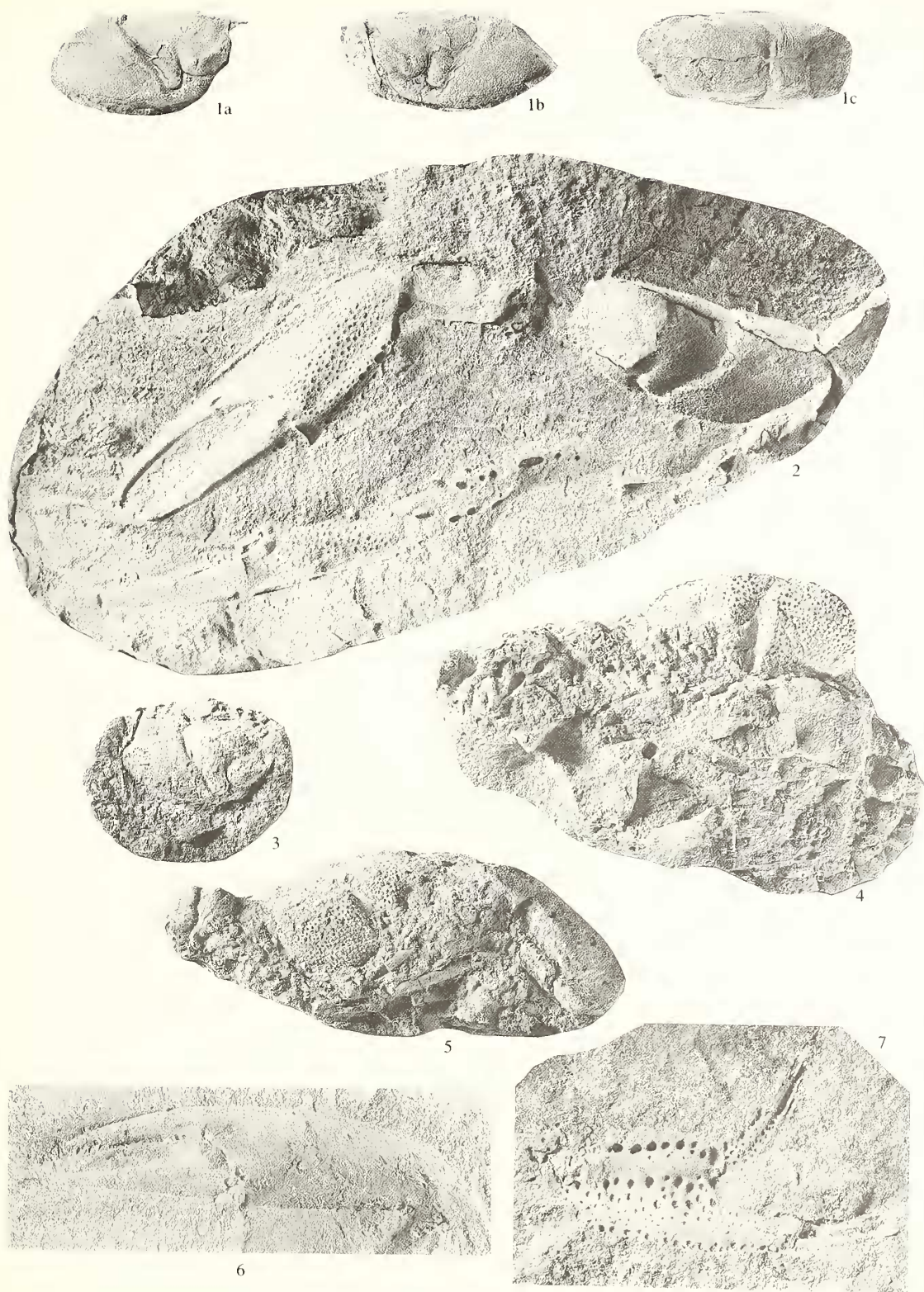
1981a *Palaeastacus* sp., Aguirre Urreta and Ramos, p. 609, pl. 2, figs. b–d.

1985b *Hoploparia* sp., Aguirre Urreta, pl. 2, figs. c–d.

Material and localities. Two left (CPBA 10856 and 10859) and one right cheliped (CPBA 10857) from locality 17, one right cheliped (CPBA 10854) from locality 16 and a pair of left and right chelipeds (CPBA 10858 a and b) from locality 18.

EXPLANATION OF PLATE 58

Hoploparia stokesi (Weller). 1a–c, two lateral and a dorsal view of cephalothorax, CIRGEO 983. 2, external impression showing cephalothorax and both chelipeds, CIRGEO 1020. 3, lateral view of cephalothorax, CIRGEO 984. 4, lateral view of CIRGEO 981 showing cephalothorax, abdomen and fragmentary pereopods. 5, lateral view of CIRGEO 980 with cephalothorax, first two abdominal segments and fragmentary pereopods. 6, impression of left cheliped, CIRGEO 986a. 7, impression of left chelae CIRGEO 987, locality 30. All figures $\times 1$.



AGUIRRE URRETA, *Hoploparia*

Description. Propodus subtriangular, longer than wide, with subparallel margins, widening slightly distally, cross section oval. Internal margin with two rows of 12 spines directed anteriorly. External margin with only one row of rounded spines bounded by a shallow furrow. Surface of propodus covered by tubercles and spines, arranged in longitudinal, parallel rows, being the larger on the centre.

Dactylus and pollex slightly shorter than palmar portion of propodus. Dactylus straight, pollex curved, both with rounded section, tips turned to meet. Cutting edges with very strong, rounded teeth. Surface covered with dense and evenly spaced, rounded tubercles. External margins of both fingers with small spines directed anteriorly.

Remarks. It is a pity that only remains of chelae are preserved of this species of *Hoploparia*. This fact prevents the comparison with most species and thus no specific assignment is proposed, although the chelae show features characteristic of their own. They can be distinguished from any other species of the genus by their strong, equal, and rounded teeth on the cutting edges.

H. longimana (Sowerby), most closely resembles the material described here, but the fingers seem to be longer and the teeth of the cutting edges are smaller and less regular in that species (Sowerby 1826, p. 493, pl. 18; Woods 1931, p. 90, pl. 5, fig. 5; pl. 6, fig. 2a, see also above). Another species that shows the same kind of chelipeds is *H. falcifer* Fritsch (Fritsch and Kafka 1887, p. 37, pl. 5, figs. 3b–c, 4–5), but the teeth are more irregular and smaller. Some overall resemblance can be seen in the original drawing of *Hoploparia* sp. n. Schlüter (1879, p. 596, pl. 16, fig. 3) from the Lower Senonian of Salzburg, especially in the shape of the teeth of the cutting edges.

It must be noted here that both left and right chelae have the same pattern of teeth and shape, unlike other species of the genus that are heterochelous.

Occurrence. All the available material comes from the upper levels of the Río Mayer Formation, of upper early to late Aptian age.

Hoploparia sp. B

Plate 57, figs. 8–10

1985b *Hoploparia* sp., Aguirre Urreta, pl. 2, fig. B.

Material and localities. Three fragmentary first pereiopods (MLP 216 a–b, 306, J. Frengüelli coll.) from locality 5, Neuquén Basin.

Description. Carpus small, subtriangular; inferior side flat and superior convex; external margin with a row of four rounded tubercles; internal margin shows three rows of irregularly spaced, larger tubercles; rest of surface punctate.

Palmar portion of propodus long, narrow (length/width: 2.74) widening distally, with oval cross-section. Upper part ornamented with evenly spaced punctae. A row of small tubercles extends from base of dactylus to base of propodus. Inferior side only punctate. The external border has a rounded ridge or carina bounded by a furrow on the inferior side. Inferior border also has a ridge bounded by a narrow furrow on inferior surface. The ridge shows at least 7 tubercles of similar size.

Two articular teeth can be seen on the base of dactylus which is broken, showing a depressed section and only one tooth on the opposite margin with the pollex, which is also missing.

Remarks. The main purpose of describing this specimen is its stratigraphic position, as it is associated with the ammonite *Thurmaniceras* sp. of the Berriasian–early Valanginian. As far as the author knows, this is the oldest record of the genus *Hoploparia*.

It is described in open nomenclature due to the scarcity of the material. I consider it unwise to erect a new species on this basis. Other more or less well defined Neocomian species are *H. aspera* Harbort, *H. dentata* (Roemer), *H. edwardsi* Robineau-Desvoidy, *H. riddlensis* Feldmann and *H. triboleti* Borrisjak.

H. columbiana Beurlen from the Neocomian of Columbia (Beurlen 1934, p. 132, pl. 25, figs. 4a–b) is only known from an incomplete carapace and may not even be a member of Nephropidae but may belong to the Mecochiridae. Many very imperfectly known Neocomian species of the genus

were considered as synonyms of *H. edwardsi* Robineau-Desvoidy by Woods (1931, p. 87) and van Straelen (1936b, p. 472).

H. dentata (Roemer) as described by Stolley (1924, p. 416, pl. 13, figs. 2–13; text-fig.) differs from *H. sp. B* by the presence of big spines on both the external and internal margins and the relatively more square propodus. The chelipeds of *H. aspera* Harbort are only known from a small imperfectly preserved fragment (Harbort 1905, p. 19, pl. 2, fig. 5c).

As far as can be interpreted from the original drawings, *H. edwardsi* Robineau-Desvoidy (including all the synonyms) seems to be very similar to *H. dentata* (Roemer) and differs from *H. sp. B* in the more square propodus, presence of spines in both margins and absence of a carina on the external border (Robineau-Desvoidy 1849).

H. riddlensis Feldmann is the best known Neocomian species and its chelipeds are similar to those of *H. sp. B* (Feldmann 1974, p. 586, pl. 1, figs. 1–8), but the carpus is longer and ornamented with a single spine on the outer surface. The propodus is relatively shorter, with spines on the outer margin, but not in the inner as preserved in the specimen here described, which also shows a carina on the external margin.

H. triboleti Borrisjak, from the Neocomian of Crimea (Caucasus), is very close to *H. dentata* (Roemer) and can be separated from *H. sp. B* by its shorter propodus, with flattish sides, external border with a carina bounded by two grooves and presence of six strong spines on the internal border (Borrisjak 1904, p. 411 and 420, pl. 13, fig. 1).

The most similar species morphologically, although of different stratigraphic occurrence, seems to be *H. sculpta* Secretan from the Albian of Madagascar (Secretan 1964, p. 105, pl. 4, fig. 11; pl. 9, figs. 1–4, 12; pl. 10, figs. 2, 5–9; text-figs. 56–58, 59–3). The slight differences are the presence of only 3 or 4 spines on the internal margin and the rim that bounds the articulation between the dactylus and propodus as well as the two tubercular processes over that rim.

Occurrence. The specimens are associated with the ammonite *Thurmaniceras* sp., from Berriasian–early Valanginian beds of the Mulichinco Formation.

Infraorder PALINURA Latreillé, 1803
Superfamily GLYPHEOIDEA Winckler, 1883
Family GLYPHEIDAE Winckler, 1883
Genus GLYPHEA von Meyer, 1835

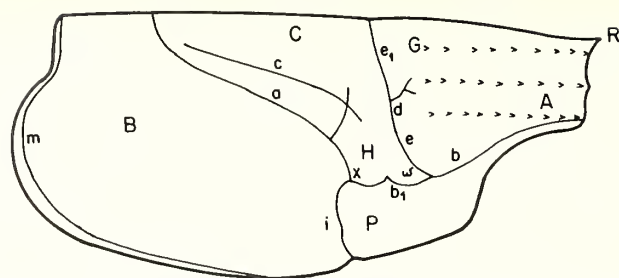
Type species. *Palinurus regleyanus* Desmarest 1822, by original designation.

Diagnosis. Carapace subcylindrical, with short pointed rostrum, two, three or more tuberculate keels on anterior region, cervical groove deep, postcervical and branchiocardiac grooves deep and very oblique, sometimes joined at different points, gastroorbital groove present in some species, other small grooves may occur, branchiostegite with anterior extension, first pereopod subchelate, carapace ornamented with granules, tubercles and pits (van Straelen 1925; Woods 1926; Glaessner 1969).

Comments. *Glyphea* is a common Jurassic genus known from many species with a wide distribution. In the Cretaceous it is much less diverse but still widespread. The other subgenus, *Squamosoglyphea*, can easily be separated because of its carapace with scale-like sculpture and its restriction to the late Jurassic of Europe (Glaessner 1969).

Trachysoma Bell can be distinguished from *Glyphea* in the shape of the cephalothorax which is long and narrow, and the straight cervical, postcervical and branchiocardiac grooves (Bell 1863; Glaessner 1969). Quayle (1987) showed that the shape and proportions of the cephalothorax of the type species, *T. scabra* Bell, compared well with *Glyphea* after preparation, and consequently he assigned that species to the genus *Glyphea*.

The other representatives of the family Glypheidae include two Triassic genera: *Litogaster* von



TEXT-FIG. 14. Sketch figure of a generalized glypheid with the main morphological features of the cephalothorax.

Meyer and *Triasiglyphea* van Straelen, and the unique living genus *Neoglyphea* Forest and Saint Laurent. *Litogaster* differs from *Glyphea* in the thin-shelled carapace with parallel postcervical and branchiocardiac grooves (Glaessner 1969; Schram 1971). *Triasiglyphea* resembles *Litogaster* but is poorly known (van Straelen 1936c). The living genus *Neoglyphea* differs from *Glyphea* in its long, narrow cephalothorax and the reduction of cephalic grooves and anterior keels (Forest and Saint Laurent 1975; 1981).

Cretaceous records of *Glyphea* are from the early Cretaceous of Antarctica (Taylor 1979), Australia (Woods 1957; Hill *et al.* 1968), Canada (Feldmann and McPherson 1980), Great Britain (Bell 1863; Woods 1927), Tanzania (Beurlen 1933) and the late Cretaceous of Central Europe (Fritsch and Kafka 1887), Great Britain (M'Coy 1854; Woods 1927), North America (Rathbun 1923) and Sweden (Danian?, Schlüter 1874; text-figs. 21 and 22).

Glyphea oculata Woods, 1957

Plate 59, figs. 1–3; text-fig. 15

1957 *Glyphea oculata* Woods, p. 162, pl. 4, fig. 4, text-fig. 4.

1985b *Glyphea oculata* Woods; Aguirre Urreta, pl. 1, figs. A–C, text-fig. 3.

Material and locality. A nearly complete specimen (CPBA 13912 A–B), and two external moulds of cephalothoraces (CPBA 13910–11) from locality 17.

Description. Cephalothorax subcylindrical, tapering anteriorly, small (length measured from base of rostrum to posterior end along mid-dorsal line: 32 mm). Maximum height 13 mm, just posterior to the mid point. Rostrum small, upturned at tip. Antennal region bordered posteriorly by cervical groove and ventrally by antennal groove. Mid-dorsal keel not well defined in available material. Three narrow, nearly parallel keels on each side, tending to diverge posteriorly; separated by broad spaces and covered with small and rounded tubercles. The spaces between the keels are smooth except for some small tubercles placed ventrally to the third keel. Cervical groove deep, oblique and almost straight. Antennal groove shallower than cervical and directed upward to meet the anterior margin. Inferior groove visible but not sharply defined, posteriorly bordering pterigostomial region, ornamented by small, rounded, densely and regularly spaced tubercles. Hepatic region small and bilobated, dorsally limited by shallow oblique groove. Ventrally hepatic groove deep forming a 'w'. Entire region less ornamented than the rest of cephalothorax. Cardiac region ornamented with coarse, rounded tubercles arranged in oblique rows, limited ventrally by the postcervical groove which is not well defined throughout and diverges from the branchiocardiac at a short distance from the mid-dorsal line; dorsal part shallow and anterior part deeper and more distinct than dorsal one.

The branchiocardiac (a) starts from dorsal line at half the distance from posterior end to the cervical groove, near the median line transverse but soon bends forward. Branchiocardiac region gently convex, with numerous rounded small tubercles, which diminish in size toward ventral margin. Edge of cephalothorax with a marginal groove and ridge. Abdominal terga rounded, nearly smooth, with two furrows bordering anterior and posterior margins. Pleural borders rounded, each pleuron with two longitudinal furrows above and with a marginal rim limited by a groove.

TEXT-FIG. 15. Diagrammatic sketch of the cephalothorax of *Glyphea oculata* Woods showing the anterior keels and cephalic grooves, $\times 1.0$.



Remarks. The pattern of the grooves of the cephalothorax compares well with that of the holotype and unique specimen of *Glyphea oculata* Woods (1957, pl. 4, fig. 4; text-fig. 4) from the late Albian of Australia. The completeness of the Patagonian material allows a better knowledge of the species as the abdomen was previously unknown. The only apparent difference between the Australian and Patagonian material seems to be in the stronger sculpture of the former. As the strength of the ornamentation varies within the Patagonian specimens, it does not seem to be a significant feature at the specific level.

Taylor (1979) included the species in the genus *Trachysoma* Bell, but the characteristics of the genus given by him, such as the acute antennal angle; parallel arrangement of a and c and smooth area between carinas, are not exclusive to it. A smooth area between keels is typical of a group of species of *Glyphea* (see Feldmann and McPherson 1980, p. 10). A parallel arrangement of a and c is not present in the holotype of the type species of *Trachysoma*, *T. scabrum* Bell (1863, pl. 10, fig. 11, see also Quayle 1987, pl. 64, figs. 12–14, text-fig. 5b) and there are no notable differences between the antennal angle of *Trachysoma* and *Glyphea* (see Taylor 1979, text-figs. 3a, d). The species is thus maintained in *Glyphea* as proposed by Woods (1957).

G. oculata Woods differs from *G. alexandri* Taylor as the latter species lacks a postcervical groove. The Antarctic species also shows the hepatic groove straight and not curved as in *G. oculata*. The inferior groove does not join the ventral but the anterior border and keels are nearly straight (Taylor 1979, p. 9, text-fig. 3a). *G. georgiensis* Taylor resembles *G. oculata* in the pattern of the grooves, but the antarctic species is larger, the cephalothorax is more elongate and it presents a transverse groove linking c with the mid-dorsal line. Stronger ornament of the abdomen of *G. georgiensis* is also noticeable (Taylor 1979, p. 11, text-fig. 3b).

G. arborinsularis Etheridge differs from *G. oculata* in its size, the stronger ornament of the cephalothorax, the nearly straight keels, the deeper antennal groove, and the less developed postcervical groove (Etheridge 1917, p. 8, pl. 1, fig. 6; pl. 2, figs. 2 and 3; Woods 1957, p. 160, pl. 4, figs. 2 and 3; text-fig. 3).

G. hennigi Beurlen from the Neocomian of East Africa is distinguished from *G. oculata* by its size, straight hepatic groove, poor development of c, presence of a transverse groove joining a and c and more convex branchial region (Beurlen 1933, p. 92, figs. 3–4).

As far as the author knows, only three species of *Glyphea* have been recorded from Upper Cretaceous deposits. *G. carolinensis* Rathbun from the Campanian of North America (Rathbun 1923, see also Feldmann 1981) is so poorly preserved as to prevent any comparison. *G. bohemica* Fritsch (Fritsch and Kafka 1887, p. 23, pl. 8, figs. 1–8; text-fig. 45), from the Turonian of Bohemia, known from Kafka's drawings, differs from *G. oculata* in its subtriangular cephalothorax, keels converging to the rostrum, different configuration of cephalic grooves, spiny pereopods and poor development of abdominal pleura. *G. lundgreni* Schlüter from the late Cretaceous?–Danian of Sweden shows an overall resemblance to *G. oculata*, but it seems to be more sculptured, with very well developed cephalic keels, absence of gastroorbital groove and different shape of postcervical groove (Schlüter, 1874, p. 48, pl. 3, figs. 3–5).

Note here *G. oculata* Woods and other Cretaceous species resemble Jurassic species more than the unique living form, *Neoglyphea inopinata* Forest and Saint Laurent, which shows a great reduction of the grooves and cephalic keels (Forest and Saint Laurent 1975; 1981).

Occurrence. *G. oculata* Woods is known from the late Albian Tambo Formation of central Queensland, Australia (Woods 1957) and from Santonian levels of the Mata Amarilla Formation of southern Patagonia, Argentina.

Glyphea sp.

Plate 59, fig. 4; text-fig. 16

Material and locality. One specimen consisting of the right side of cephalothorax and five partially preserved pereopods (CPBA 14096, A. Gutiérrez coll.) from locality 4.

Description. Cephalothorax subcylindrical, narrowing in front. Rostrum not well preserved. Anterior region from base of rostrum to mid-dorsal end slightly more than one third the length of carapace. Cervical groove (c-e₁) deep, nearly straight, dorsal part curving slightly backward and ventral part slightly forward. Near ventral margin, cervical groove joins antennar groove (b), which coincides with ventral border of anterior region. Gastroorbital groove (d) arises from the cervical groove. At first it is nearly horizontal, but then it divides into two branches, one directed dorsally, the other ventrally. Three longitudinal keels on each side of the anterior region. The mid one originates from the point of division of d. The most prominent keel developed below the ventral branch of d, bearing small rounded tubercles. Upper keel not well preserved but starts above the upper end of dorsal portion of gastroorbital groove. Spaces between keels are concave and nearly smooth. Epistome preserved, as well as part of the third maxilliped.

Cardiac region poorly preserved, postcervical groove (c) cannot be seen. Branchiocardiac groove (a) extends obliquely forward from dorsal line, ventrally joining inferior (i) groove and the hepatic (b₁) which in turn bounds the hepatic lobe. Pterygostomial region subquadrate, covered with small rounded tubercles. Branchiocardiac region broadly convex, crushed on dorsal part, ornamented with small tubercles, more densely spaced on the dorsal part. Tubercles scattered near ventral margin, also smaller. Posterior and ventral border with marginal groove and ridge.

First to fifth right pereopods partially preserved, articulated with cephalothorax. Distal end not visible. Merus of first one large, flat, ornamented with small pits. Other pereopods decreasing in size up to the fifth which is very thin and nearly smooth.

Remarks. The specimen described shares characters with both Jurassic and Cretaceous species. It compares well with Jurassic species such as *G. regleyana* (Desmarest) or *G. rostrata* (Phillips) particularly in the well-defined gastroorbital groove. It also resembles Cretaceous species such as *G. cretacea* or *G. oculata* Woods, as well as other Neocomian species, in the distribution and shape of the cephalic grooves which are less well developed than in the Jurassic species. This tendency is confirmed by the unique living species of the family, *N. inopinata* Forest and Saint Laurent, which shows relict keels, and has the gastroorbital and postcervical grooves nearly absent (Forest and Saint Laurent 1975, p. 155, pls. 1 and 2).

G. regleyana (Desmarest) differs from *G. sp.* in its bigger overall size as well as the relatively larger anterior region, stronger ornament and the antennar groove which runs obliquely to the ventral margin and not coincident with it as happens in the Argentinian species (Woods 1925, p. 57, pl. 14, figs. 3-5; text-fig. 7A, van Straelen 1925, p. 183, fig. 89).

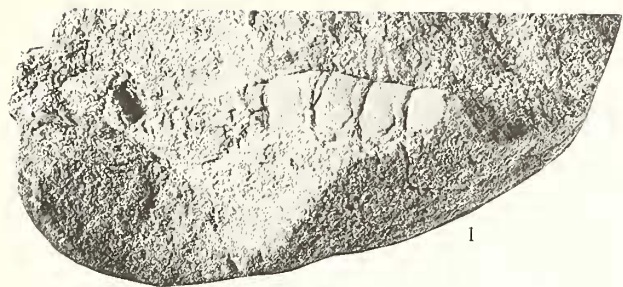
G. rostrata (Phillips) resembles *G. sp.* in its small size, relatively small anterior region, and antennar groove nearly coincident with the antero-ventral margin. However, it differs in the poor

EXPLANATION OF PLATE 59

Figs. 1-3. *Glyphea oculata* Woods. 1, left lateral view of CPBA 13912, showing partially preserved cephalothorax and abdomen. 2, right lateral view of CPBA 13911 showing anterior part of cephalothorax. 3, left lateral view of impression of cephalothorax showing disposition of cephalic grooves, CPBA 13910, locality 17.

Fig. 4. *Glyphea* sp. Right lateral view of CPBA 14096 showing cephalothorax and proximal portion of pereopods, locality 4.

Figs. 5-8. *Meyerella rapax* (Harbort). 5, lateral view of specimen with partially crushed cephalothorax, first three abdominal segments and basal articulation of pereopods, MLP 19835. 6, lateral view of crushed cephalothorax and part of pereopods, CPBA 13214. 7, lateral view of specimen showing cephalothorax and abdomen, MLP 19834. 8, lateral view of cephalothorax, first abdominal segments and merus of pereopod, MLP 19836, locality 3. All figures $\times 1$.



1



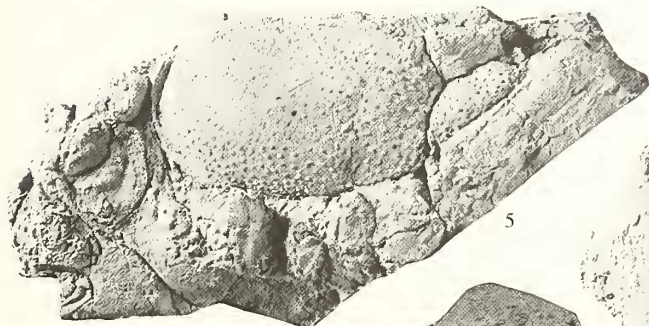
2



3



4



5



6



7



8



TEXT-FIG. 16. Diagrammatic sketch of *Glyphea* sp. showing the cephalic keels and grooves, $\times 1.0$.

development of d, which is restricted to a short horizontal groove, and in the stronger keels and ornament (Woods 1925, p. 57, pl. 15, figs. 4–10; text-fig. 7B).

Other Neocomian species are *G. jeletzkyi* and *G. robusta* Feldmann and McPherson spp., *G. henningi* Beurlen, *G. alexandri* and *G. georgensis* Taylor spp.

G. robusta has strong ornamentation on the branchiostegite, also a very well developed postcervical groove and no gastroorbital groove (Feldmann and McPherson 1980, p. 8–11, pl. 2, figs. 8 and 9; pl. 3, figs. 2–7; text-figs. 3–5). *G. jeletzkyi* shows a subquadrate cephalothorax with well developed, subparallel postcervical and branchiocardiac grooves. The cervical groove is nearly vertical and the antennal keels are inclined and would intersect the ventral margin.

G. alexandri Taylor can be separated from *G. sp.* by its size, much more strongly sculptured carapace, and different pattern of grooves, especially the poor development of the branchiocardiac groove (Taylor 1979: 8, pl. 1a–e; text-fig. 3a). *G. georgensis*, another Antarctic Neocomian species, can be distinguished from *G. sp.* by its size, more sculptured carapace, which is also long and narrow, and by the better development of the postcervical groove (Taylor 1979, p. 10, pl. 1f–g; text-fig. 3b).

G. henningi Beurlen (1933, p. 92, text-figs. 3 and 4) has a more rounded cephalothorax with a groove that connects a and c and seems to reach the mid-dorsal line (text-fig. 3) and also a different shaped inferior groove. The ornamentation and the development of the gastroorbital groove are quite similar to that of *G. sp.*

G. cretacea McCoy differs from *G. sp.* in its relatively larger anterior region, keels convergent to the back, area below lower keel covered with tubercles, antennar groove not coincident with the antero-ventral margin, and absence of gastroorbital groove (McCoy 1854, p. 118, pl. 14, fig. 2; Woods 1925, p. 61, pl. 16, figs. 3–5).

G. sp. differs from *G. oculata* Woods in its well-developed gastroorbital groove, keels which are straight and not convergent, smaller anterior region and in having the antennar groove coincident with the antero-ventral margin (Woods 1957, p. 162, pl. 4, fig. 4; text-fig. 4; Aguirre Urreta 1985b, pl. 1, figs. A–C; text-fig. 3).

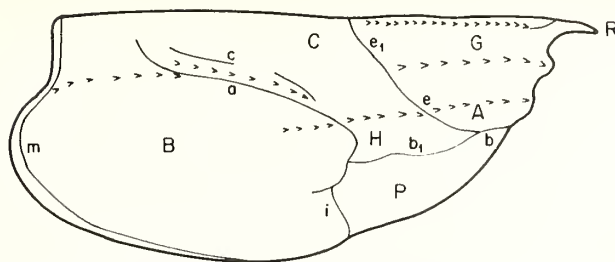
Occurrence. The species occurs in the upper member of the Agrio Formation, slightly above the level with *Crioceratites andinum* (Gerth) of late Hauterivian–early Barremian age (Riccardi 1984).

Family MECOCHIRIDAE van Straelen, 1925

Genus MEYERELLA Simpson, 1985

Type species. *Meyerella magna* McCoy 1849, by original designation.

Comments. Simpson (in Simpson and Middleton 1985) erected the new genus *Meyerella*, and selected *Meyerella magna* as its type species in his Ph.D. thesis. Unfortunately the paper in which he formalized this genus is still in press, so there is little that can be said about the new genus and no diagnosis is given here. Its main morphological features, together with the differences from *Meyerella*, are given in Simpson and Middleton (1985). According to this work, and taking account of the similarities between *M. rapax* and *M. magna*, I assume that the former species belongs to the new genus *Meyerella*. *Meyerella* seems to be represented in the Cretaceous of Germany (Harbort 1905; Kemper 1976), Great Britain (Bell 1863; Woods 1928; Simpson and Middleton 1985), Mexico (Rathbun 1935), South Africa (Kitchin 1908), Spain (van Straelen 1927; Via 1975), Tibet (Wang 1981) and Argentina (herein) (see text-figs. 21 and 22).



TEXT-FIG. 17. Sketch figure of a generalized mecochirid showing the main morphological features of the cephalothorax (modified from Wang 1981 and Simpson and Middleton 1985).

Meyerella rapax (Harbort, 1905)

Plate 59, figs. 5–8; text-figs. 18 and 19

- 1863 *Astacodus falcifer* (Phillips) Bell, p. 30, pl. 9, fig. 3 only.
 1905 *Meyerella rapax* Harbort, 1905, p. 11, pl. 1, fig. 12; pl. 2, figs. 1–4, pl. 3, figs. 1 and 2, pl. 11, figs. 1 and 2.
 1928 *Meyerella rapax* Harbort, Woods, p. 70, pl. 18, figs. 25, 6, 27, 8.
 1932 *Meyerella rapax* Harbort, Glaessner, p. 58.
 1976 *Mecochirus rapax* (Harbort); Kemper, pl. 11, fig. 1
 1985b *Meyerella rapax* Harbort, Aguirre Urreta, pl. 1, figs. D–G.

Material and locality. Nine specimens (MLP 19834–40, CPBA 13913–14) from locality 3.

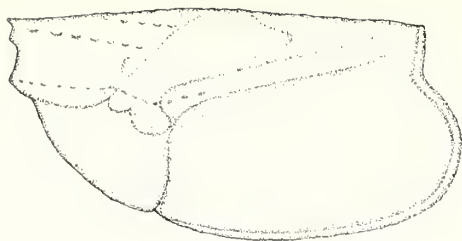
Description. Cephalothorax relatively large, subcylindrical, tapering anteriorly, sides of thorax convex; rostrum short, poorly preserved. Antennal region with three lateral keels and a less developed dorsal keel. The middle and lower keel are stronger and bear coarse tubercles, while the upper keel is less defined, with smaller tubercles. Spaces between keels smooth. Cervical groove deep, narrow, directed obliquely forward and forming an angle of 45° with the mid-dorsal line, joining antennal groove (b) which is well defined and runs nearly parallel to the mid-dorsal line. Branchiocardiac (a) groove well defined, sinuous, nearly reaching the posterior margin or carapace. Postcervical groove (c) almost parallel to branchiocardiac, but less distinct. An ill defined sinuous lobe diverges from the postcervical groove, cutting the mid-dorsal line. The third and lower keel of the anterior region is continued on the lobe over the hepatic region and between the branchiocardiac and postcervical grooves. Hepatic lobe (h₁) with a 'w' shape. Inferior groove (i) curved, cutting ventral border at same place as cervical, with the mid-dorsal line.

Pterygostomial region with small, sparse, rounded tubercles; cardiac region with strong upper tubercles, decreasing in size and density toward postcervical groove. Branchiocardiac region with small, dense and forwardly directed spines. Scanning electron micrographs (text-fig. 19) of carapace show detailed structure of tubercles. Posterior and ventral border with marginal furrow, less prominent towards anterior part.

First five abdominal segments are preserved, tail fan missing. Terga arcuate, with well-developed anterior grooves and less marked posterior ones; both parallel to their respective margins. Surface nearly smooth, only ornamented by small tubercles on dorsal region. A transverse furrow separates terga from pleura. The latter are subtriangular, rounded, the second is the largest, with the antero-ventral border rounded and the postero-ventral straight and subvertical. The whole margin is denticulated. Pleura three to five decreasing in size and triangular. Pereiopods partially preserved usually showing basal articulation. Some fragments may correspond to merus of first pereiopods due to their position and size.

Remarks. The specimens studied agree closely with the originals of Harbort (1905, pl. 1, fig. 12; pl. 2, figs. 1 and 2, pl. 3, figs. 1 and 2; pl. 11, fig. 12) in size, configuration of grooves, shape of cephalothorax and ornament.

In the Austral hemisphere, only one species of *Meyerella* is known: *M. schwarzi* (Kitchin) from the Neocomian of South Africa. This species closely resembles *M. rapax* in relative proportions, ornament, pattern of the grooves and stratigraphic level, but *M. schwarzi* is smaller, with the cephalothorax more compressed, and it presents a well marked sigmoidal groove connecting c with



TEXT-FIG. 18. Diagrammatic sketch of the cephalothorax of *Meyerella rapax* (Harbort) showing the characteristic disposition of grooves, $\times 1.0$.

the dorsal margin (Kitchin 1908, p. 212, pl. 8, fig. 22, pl. 9, fig. 4, 4a, 5, pl. 10, fig. 4, 4a, 4b). It also lacks the denticles present in the anterior border of the abdominal pleura in *M. rapax*. Other closely related species, such as *M. mexicana* (Rathbun, 1935b = *M. magna* according to Simpson and Middleton 1985), *M. bolivarii* (van Straelen, 1927) and *M. magna* (McCoy, 1849), differ from *M. rapax* in their stronger ornament of the cephalothorax as well as in the abdominal terga, and in the poor development of the inferior and postcervical grooves (see also Woods 1928; Via 1975; Wang 1981).

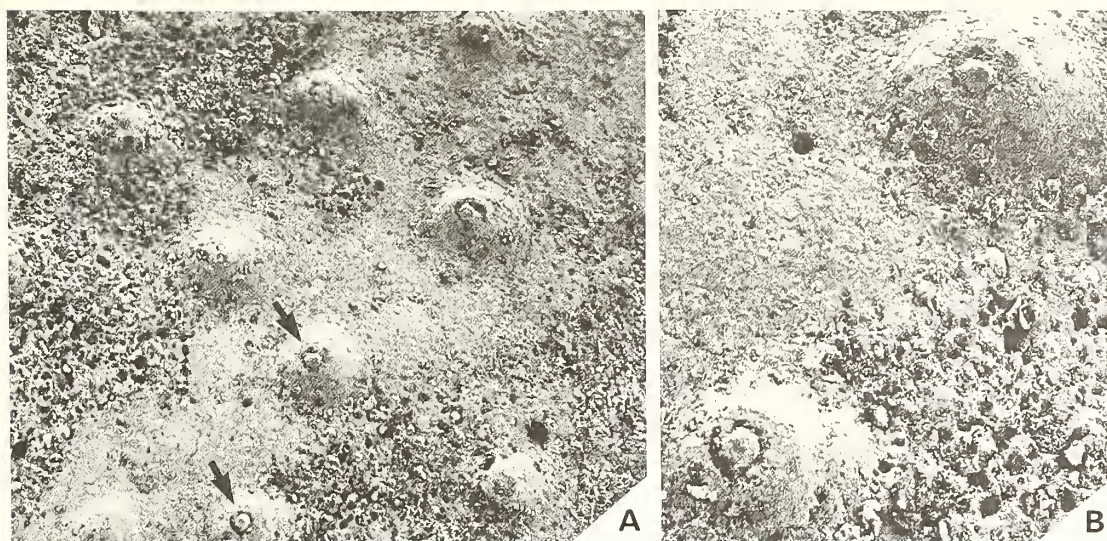
It is interesting to note that the structure of the tubercles of the cephalothorax, as seen by scanning electron micrographs is very similar to that observed in *M. magna* (see Simpson and Middleton 1985, fig. 7h) and completely different from the tubercles associated with pores present in *Meyerella ornata* (Simpson and Middleton 1985, fig. 7f-g).

The only other record of a mecochirid from South America is that of *Mecochirus chilensis* Förster from the Kimmeridgian of Northern Chile (Förster and von Hillebrandt 1984). The author had the opportunity of comparing the Patagonian material with specimens of *M. chilensis* deposited in the Museum of the Universidad del Norte, Antofagasta, Chile. *M. chilensis* resembles *M. rapax* in the development of an hepatic crest, but it is much smaller, shows great inflation of the branchiocardiac region which is very large in comparison with the anterior region, and a poor development of the inferior groove (Förster and von Hillebrandt 1984, p. 73, pl. 2, figs. 1-8, pl. 3, figs. 1 and 2, text-figs. 3-7).

Other supposed mecochirids from South America were the records of *Peuhenchia tellecheai* and *P. magna* Rusconi spp., from ?Middle Jurassic beds of Arroyo Cajón Grande, southern Mendoza, Argentina (Rusconi 1945). The holotype and unique specimen of *P. tellecheai* is a crushed small specimen preserved in black shales, which was studied by this author during a visit to the Museo de Historia Natural de Mendoza. The morphology of the anterior region was misinterpreted by Rusconi (1945, figs. 1 and 2), and taking in account the absence of diarsis in the uropods and the very bad preservation I can only state that it is probably not a mecochirid, but a callianassid. *P. magna* is also represented by a couple of crushed chelae and it, too, is a callianassid. The age of the strata bearing these specimens (Vaca Muerta Formation) is currently considered to be late Jurassic-Berriasian (Nullo 1987).

In the collections of the Universidad de Buenos Aires, there is a German specimen of *M. rapax* from Sachsenhagen i. Schaumburg-Lippe (early Valanginian, E. Stolley coll. N° 900) which is identical with the material studied here, except for its larger size. I have also had the opportunity to see a large collection of *M. rapax* (P. Rawson coll.) from the earliest Barremian Tealby Limestone, of Nettleton, Lincolnshire, England, and the specimens compare very well with the Argentinian material.

Occurrence. *M. rapax* is known from the early Valanginian of Müsingen and Gronau, Westphalia, Northern Germany (Harbort 1905; Glaessner 1932); the C₁ and probably C₉ beds of Speeton Clay, Hauterivian; and Tealby Clay, Lincolnshire, England (Woods 1928) and the *Olcostephanus curacoensis* assemblage zone of the Mulichinco Formation, at the Valanginian-Hauterivian boundary (Riccardi 1984).



TEXT-FIG. 19. Scanning electron micrographs showing ornament of anteroventral region of branchiostegite of *Meyerella rapax*. A, general view, $\times 50$. B, detail of two tubercles, as arrowed in A, $\times 120$.

Infraorder ANOMURA H. Milne-Edwards, 1832
 Superfamily THALASSINOIDEA Latreille, 1831
 Family CALLIANASSIDAE Dana, 1852
 Subfamily PROTOCOLLIANASSINAE Beurlen, 1930
 Genus PROTOCOLLIANASSA Beurlen, 1930

Type species. *Callianassa archiaci* A. Milne-Edwards 1860, by original designation.

Diagnosis. Callianassid with linea thalassinica, first pereopod chelate, heterochelous, abdomen with well-developed pleura, uropods without diaeresis (Glaessner 1969).

Comments. The subfamily Protocallianassinae is presently represented by the unique extinct genus *Protocallianassa*. *Protocallianassa* Beurlen and *Callianassa* Leach are not easy to separate when only the chelae are preserved, as is usually the case. In spite of that, Mertin (1941, p. 199) gave some features as characteristics of the chelae of *Protocallianassa* which allow separation of the two genera. They are: 1) narrow shape of the palm; 2) diagonal union of propodus and carpus; 3) absence of an indentation in the anterior edge of the palm; 4) carpus thinner than, and usually as long as, the propodus, and 5) absence of a lateral extension on the merus.

According to Beikirch and Feldmann (1980) placement in one or other genus is mostly based in stratigraphic position. Late Cretaceous forms are assigned to *Protocallianassa* while the Tertiary species are placed in *Callianassa*. This is not always the case, e.g. *C. peruviana* Rathbun (Rathbun, in Knechtel *et al.* 1947) is an Albian species, *C. meridionalis* Ball is from the Late Cretaceous of Antarctica and *C. burckhardti* Böhm from the Cretaceous-Tertiary boundary of the Neuquén Basin (see below).

The fact that the pereopods are heterochelous and that differences are noticeable in males and females, together with the usual fragmentary preservation, has led to the erection of a huge number of species in both genera. A worldwide exhaustive revision of both families is needed. As understood here, Cretaceous representatives of *Protocallianassa* are known from Antarctica (Taylor 1979), Central Europe (Mertin 1941), France (Tribolet 1873-4; 1874-5), Great Britain (Woodward 1868),

North America (Pilsbry 1901; Rathbun 1926a; 1935; Roberts 1962; Beikirch and Feldmann 1980; Bishop 1983b; 1985) and Patagonia (Aguirre Urreta 1983; 1985b; text-figs. 21–22).

Protocallianassa patagonica Aguirre Urreta, 1983

Plate 60, figs. 1–4

1983 *Protocallianassa patagonica* n. sp. Aguirre Urreta, p. 312, pl. 1, figs. *f–j*.

1985b *Protocallianassa patagonica* Aguirre Urreta, pl. 2, fig. O.

Material and localities. The holotype (CPBA 11139), three fragmentary specimens (CPBA 11667, 11138, 11670) from locality 14, and two right chelae (CPBA 11668–69) from locality 13.

Description. Ischium rectangular, twice as long as wide, merus smaller, square. Carpus triangular, with diagonal articulation with palm. Palmar portion of propodus square, flattened, external surface convex, inner surface flat. Upper margin rounded, lower border sharp, acute. All described limbs evenly ornamented with very small, obtuse, and rounded tubercles and pits. Only one specimen (CPBA 11667) shows a group of pits on external surface near the articulation with the dactylus. There are at least 12 small, rounded pits with the centre elevated like a cudgel. They probably represent the insertion of setae. Fixed finger with triangular cross-section, cutting edge with sharp tooth and carina, dactylus longer than pollex, with rounded cross-section, without tooth and/or carina.

Remarks. As the Patagonian material shows all the characteristic features given by Mertin (1941), it is placed in *Protocallianassa* and it will only be compared with Lower Cretaceous species of that genus and *Callianassa*. *P. patagonica* differs from *P. infracretacea* (Tribolet) by the lack of tooth and carina in the fixed finger of the latter species together with the presence of a line of pits in the inner border of the palm, which probably represented the insertion of setae (Tribolet 1873–4, p. 352, pl. 12, fig. 1).

In *P. neocomiensis* (Woodward), the carpus is square and the propodus is rectangular, differing from *P. patagonica* which presents a triangular carpus and square propodus. The former species has a tooth on the cutting edge of the movable finger, and not on the pollex, as in *P. patagonica* (Woodward 1868, pl. 2, fig. 5).

C. peruviana Rathbun is a very small species (35 mm length of cephalothorax and abdomen) from the Albian of Peru. Apart from the notable difference in size, *C. peruviana* can readily be separated from *P. patagonica* by the presence of spinules in the inner margin of the palm, which continue in the fixed finger, the pimple-like ornament of the outer surface of the palm, and the variable development of teeth on the cutting edges (Rathbun, in Knechtel *et al.* 1947, p. 133, pls. 48–50).

P. antarctica (Taylor) is the closest species geographically and stratigraphically. It can be distinguished from *P. patagonica* by its long fingers, variable toothing of the fixed finger and presence of a carina, in both fixed and movable fingers (Taylor 1979, p. 20, pl. 3, figs. *e–g*; text-fig. 9a–c).

Occurrence. The species occurs in the Río Mayer Formation, in the *Colchidites* assemblage zone of the late Barremian (Riccardi 1984, Aguirre Urreta and Klinger 1986).

Subfamily CALLIANASSINAE Dana, 1852

Genus CALLIANASSA Leach, 1814

Type species. *Cancer (Astacus) subterraneus* Montagu 1808, by original designation.

Diagnosis. Callianassid with linea thalassinica, first pereopod chelate, heterochelous, with subtriangular carpus, propodus rectangular, fingers short and curved, abdominal pleura rudimentary. (Slightly modified from Glaessner 1969.)

Comments. *Callianassa* is a very common fossil in Cretaceous–Tertiary deposits mostly known from its first pereopods. Recent species of the genus are widely studied because of their fossorial mode of life and their usual association with burrows and systems of tunnels in near-shore environments.

Callianassa is difficult to separate from *Protocallianassa* (see above and also Bishop 1986, p. 330), but it is easily distinguished from the other genus of the family, *Ctenocheles* Kishinouye, which possesses a very inflated palm and long, slender fingers, with comb-like teeth in the cutting edges (Secretan 1964; Glaessner 1969).

Callianassa has been recorded from Cretaceous beds of Antarctica (Ball 1960), Brazil (Beurlen 1962), Canada (Feldmann and McPherson 1980), Chile (Förster and Stinnesbeck 1987), Europe (Mertin 1941), New Zealand (Glaessner 1960), North America (Pilsbry, 1901; Rathbun 1926a; 1935; Roberts 1962; Beikirch and Feldmann 1980; Bishop 1981), Peru (Knetchel *et al.* 1947) and Argentina (Böhm 1911; Damborenea *et al.* 1979; Aguirre Urreta 1985b; text-figs. 21–22).

Callianassa meridionalis Ball, 1960

Plate 60, figs. 5–11

1960 *Callianassa meridionalis* Ball, p. 15; pl. 2, figs. 3–5.

1985b *Callianassa meridionalis* Ball; Aguirre Urreta, pl. 2, fig. N.

Material and localities. External impressions of two right and one left chelae (CPBA 14107) from locality 28 (A. López Angrimmann coll.); five pairs (CPBA 14098, 14099 A–B, 14100, 14108); three right chelae (CPBA 13915, 14102, 14105) and three left (CPBA 14101, 14103, 14104) from locality 27.

Description. Small, strongly heterochelous callianassid. Carpus trapezoidal, increasing in width towards distal end; articulation with manus straight. Manus subrectangular, with parallel margins. It shows allometric growth; the manus becomes more square as width increases more rapidly than length. Same growth pattern in fingers. When chelae are small the fingers are as long as the palm, but as size increases, the fingers tend to become relatively shorter.

Inner surface flat or slightly curved on the middle; upper margin acute, narrow, with 14–16 little spines giving the impression of a serrated border, extending on base of fixed finger. Lower margin broadly rounded with a well marked ridge on the proximity of carpus that disappears towards dactylus. Lower margin bounded by a row of 7–8 tiny, rounded pits on both inner and outer surfaces. The latter strongly convex and smooth.

Fixed finger short, straight with triangular cross-section; one very small tooth near the base on cutting edge. Dactylus strong, longer than pollex, with oval cross-section, tip curved to meet fixed finger. Surface with scattered pits.

Remarks. *C. meridionalis* Ball shows an overall resemblance with *P. patagonica*, but they can be differentiated by the flattened palm of the former, with acute and serrated outer margins and lower margins rounded with a ridge (Ball 1960, p. 15, pl. 2, figs. 3–5). The Antarctic species is strongly heterochelous, but the Patagonian species seems to have chelae of more or less the same size, although no pairs of claws were found.

C. meridionalis Ball differs from *C. burckhardti* Böhm in its smaller size, narrow palm, smoother surface without tubercles, flattened inner and outer surfaces, and triangular fixed finger with small tooth (Ball 1960; see also below).

C. symmetrica Feldmann and Zinsmeister, from the Eocene of Antarctica, can easily be distinguished from *C. meridionalis* by being weakly heterochelous, with large and subquadrate carpus, triangular dactylus and toothless, sulcate fixed finger (Feldmann and Zinsmeister 1984, p. 42, fig. 2A–D).

P. cenomaniensis (Milne-Edwards) can be distinguished from the Antarctic species by the presence of a tooth on the dactylus, and inner and outer margins of palm with denticles throughout (Milne-Edwards 1860, p. 329, pl. 14, fig. 5–5a).

Wetzel (1930) described material from the Quiriquina Formation, late Cretaceous of southern Chile, that comprises a carpus with outer margin rounded, serrated and with smooth surface, as well

as four abdominal segments all of them badly preserved. He assigned them to *Callianassa* sp. ex aff. 'd' *Archiaci*'. The author had the opportunity to examine very nicely preserved specimens from the same locality deposited in the Museum of the University of Concepción, Chile. These forms can be separated from *C. meridionalis* by the presence of a serrated keel in the fixed finger, a big tubercle in the articulation of palm and dactylus, and the serrated outer border of the palm. This material has recently been assigned to *C. saetosa* (Förster and Stinnesbeck 1987).

A species described by Glaessner (1960, p. 11, pl. 2, fig. 6) from the Maastrichtian of New Zealand, as *C. waikurana* Glaessner, can be differentiated from *C. meridionalis* by the subquadrate shape of the palm, strongly convex external surface, and toothless fixed finger.

Occurrence. The species has been recorded in the Campanian beds of the Santa Marta and López de Bertodano formations of eastern Antarctica.

Callianassa burckhardti Böhm, 1911

Plate 60, figs. 12–17

1911 *Callianassa burckhardti* Böhm, p. 39, 1 text-fig.

1985b *Callianassa burckhardti* Böhm; Aguirre Urreta, pl. 2, figs. L–M.

Material and localities. The holotype, a left palm (MLP 10744) from locality 6, two left and two right palms (CPBA 6435 a–b; 6435 c–d) from the cliffs north of General Roca 6' (P. Etchevehere coll.); seven right (CPBA 6471 a–g) and five left palms (CPBA 6471 h–l), and two carpus (CPBA 6471 m–n) from locality 9 (P. Etchevehere coll.), two right (CPBA 14121 a–b), two left palms (CPBA 14121 d–e) and one carpus (CPBA 14121 c) from locality 7 (V. Ramos coll.), and eight left (CPBA 14108 a–h) and two right palms (CPBA 14108 i–l) from an unknown locality near to General Roca (locality 6).

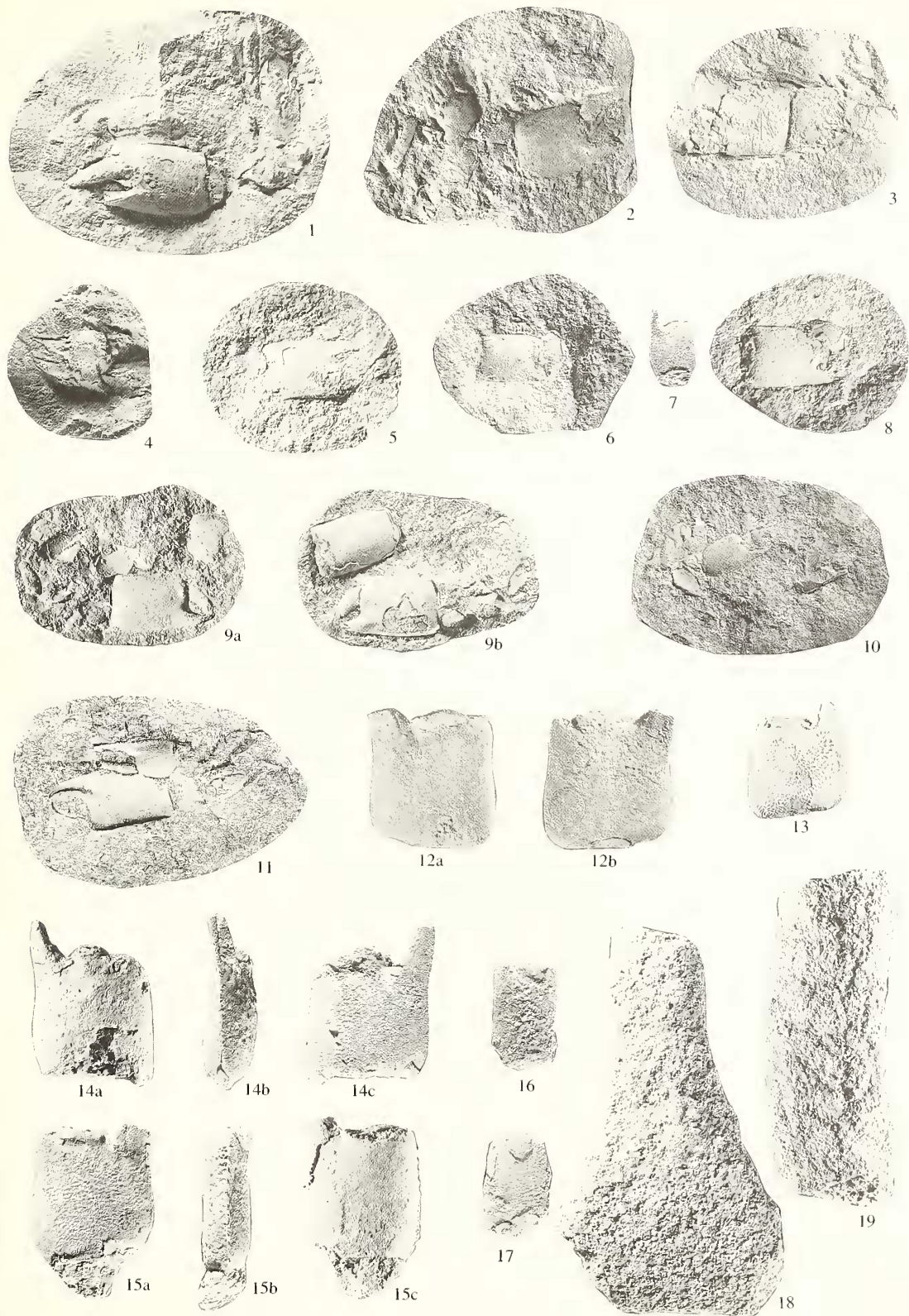
Description. Medium to large palms of callianassids. Articulation with carpus straight. Carpus large, subrectangular, with parallel margins. Cross-section oval, with curved outer and inner surface, margins acute. Small specimens subrectangular, longer than wide (L/W: 1.11–1.37), with parallel margins and oval cross-section. Large specimens with square palms, with oval but flattened cross-section. External surface rounded, ornamented with pits evenly spread over whole surface. On the internal moulds these pits appear as granules. Internal surface flattened, smoother. Inferior margin acute, slightly serrated. Upper margin also sharp, narrow, with at least 8 small spines visible on well-preserved specimens. Fixed finger short, with triangular cross-section; two lines of pits bound the cutting edge. Dactylus unknown, but its base is large, oval, elevated, with a collar rim.

Remarks. *C. burckhardti* Böhm is characterized by its large square palm, although small specimens are somewhat subrectangular. The square shape is believed to be the result of allometric growth, better shown by the pairs of *C. meridionalis* Ball (see above). Both left and right palms are indistinctively big or small, so size-related shape differences are unlikely.

C. waikurana Glaessner, from the Maastrichtian of New Zealand differs from *C. burckhardti* by

EXPLANATION OF PLATE 60

- Figs. 1–4. *Protocallianassa patagonica* Aguirre Urreta. 1, lateral view of holotype, CPBA 11139, locality 14. 2–3, lateral views of two specimens, CPBA 11668a–11669, locality 13. 4, detail of ornament of external surface, CPBA 11667, locality 14.
- Figs. 5–11. *Callianassa meridionalis* Ball. 5–6, two lateral views of pairs of chelae, CPBA 14102, 14104. 7, small right chelae, CPBA 14105. 8, lateral view of a pair of chelae, CPBA 14101. 9a–b–10, lateral views of pairs of chelae, CPBA 14099a–b, 13915. 11, lateral view of a pair of chelae, CPBA 14098, locality 27.
- Figs. 12–17. *Callianassa burckhardti* Böhm. 12a–b, two lateral views of holotype, MLP 10744, locality 6. 13, internal view of left chelae, CPBA 14108f. 14a–c, outer, inferior and internal views of CPBA 14108a. 15a–c, internal, upper and outer views of CPBA 14108b. 16–17, lateral views of CPBA 14121a–b, locality 7. 18–19, Ichnogenus *Thalassinoides*, associated with specimens illustrated in figures 16–17, locality 7. All figures $\times 1$.



its smaller size, smooth external surface and carinate lower margin (Glaessner 1960, p. 11, pl. 2, fig. 6).

The carpus described by Wetzel (1930) as *Callianassa* sp. ex. aff. '*d'Archiaci*' from the late Cretaceous of Quiriquina, southern Chile, although not illustrated, differs from the carpus of *C. burckhardti* by its serrated outer margin, in comparison with the acute, sharp but smooth margin of the latter species. Material from the same localities, recently assigned to *C. saetosa* (Förster and Stinnesbeck 1987, p. 53, pls. 1–2, pl. 3, fig. 6, text-figs. 2–3) can be distinguished from *C. burckhardti* by its rectangular propodus, presence of tooth in fixed finger and smaller carpus.

Occurrence. *C. burckhardti* Böhm has been recorded from both Maastrichtian and Danian levels in the Neuquén Basin. In one locality (Mina Ranqueles, Ramos 1981), the specimens are associated with trace fossils here assigned to *Thalassinoides* sp.

Ichnogenus THALASSINOIDES Ehrenberg, 1944

Plate 60, figs. 18 and 19

Material and locality. Several fragments of the burrow system were recovered from the Roca Formation, level III of locality 7 (V. Ramos coll.).

Description. Vertical to subvertical cylindrical burrows, transverse to bedding, straight to slightly sinuous, 15–30 mm in diameter. Cross-sections vary from almost circular to oval. Outer surface smooth or covered with low mounds (plate 60, fig. 19). Y-shaped bifurcations are common, swollen at point of branching (plate 60, fig. 18).

In thin sections, the burrow filling consists of foraminifers, mostly agglutinated forms, without planktonic elements (Malumián, pers. comm. 1986), small gastropods, spines and debris of echinoids, bivalve fragments and indeterminate shell debris. The clasts are subangular and strongly fragmented, cemented with calcite. In the thin sections studied, no lining is visible, only a micritic to subsparitic carbonate cement forms an external coating to the clastic filling. The burrows were apparently filled mechanically and the cement was formed later by partial dissolution of the carbonate material.

Remarks. Unfortunately, as is usually the case, no remains of *C. burckhardti* Böhm were found inside the burrow system. Both are associated in the same levels at locality 7 (Ramos 1981).

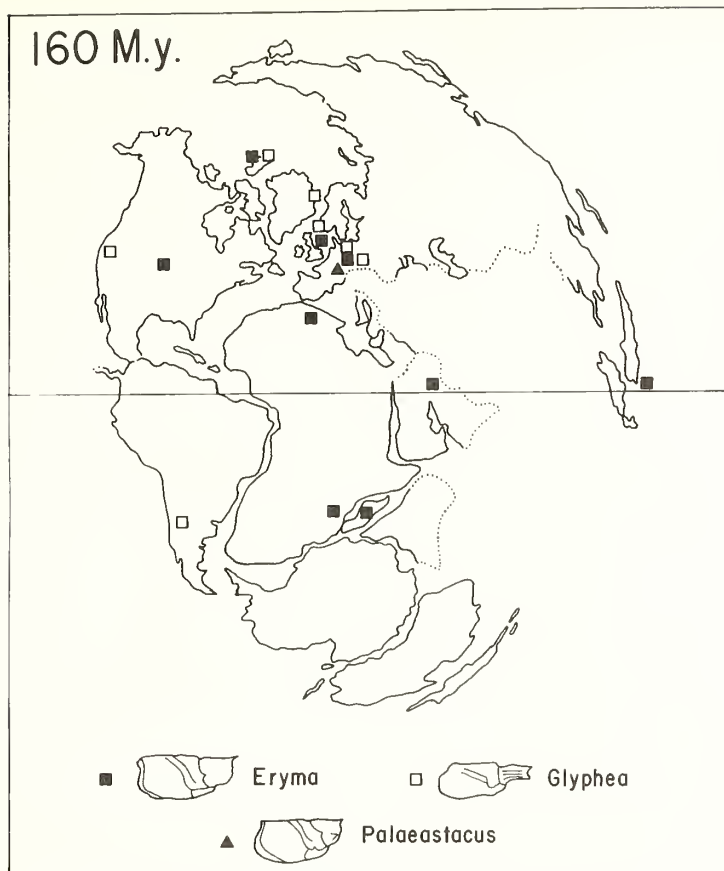
After reading the extensive bibliography presently available (e.g. Kennedy 1967; Fursich 1973; Frey 1975; Frey *et al.* 1978; Hantzschel 1975; Pemberton *et al.* 1984, among many others), the author finally decided to assign these burrows to the ichnogenus *Thalassinoides*, although the main problem of placing the trace fossil was that it shows some features of both *Thalassinoides* and *Ophiomorpha* Lundgren, 1981. As far as the author knows, vertical systems are more common in *Ophiomorpha*, but the smooth walls are typical of *Thalassinoides*. In any case, although I agree with Fursich (1973) in the difficulty of separating these ichnogenera, especially when intermediate and gradational forms are known, I adhere to the amended diagnosis of *Thalassinoides* given by Kennedy (1967, p. 132) which included both vertical and horizontal elements.

Comparison with the most common species of that ichnogenus shows differences, mainly in the predominance in the system described here, of vertical to subvertical elements, in contrast with the dominance of horizontal tunnels in *T. saxonius* (Geinitz), *T. suevicus* (Rieth), and *T. paradoxica* (Woodward).

Occurrence. The trace fossils are associated with *C. burckhardti* Böhm, *Baculites* sp., *Eubaculites* sp., *Pterotrionia windhauseniana* (Wilckens), *Pacitrionia patagonica* Feruglio, and *Gryphaeostrea callophylla* (Ihering). The fossil assemblage indicates a middle Maastrichtian age (Ramos 1981).

PALAEOBIOGEOGRAPHIC COMMENTS

A series of four palaeogeographic reconstructions (text-figs. 20–23) shows the geographical distribution of the genera studied here from the Jurassic to early Tertiary times. Note that only one



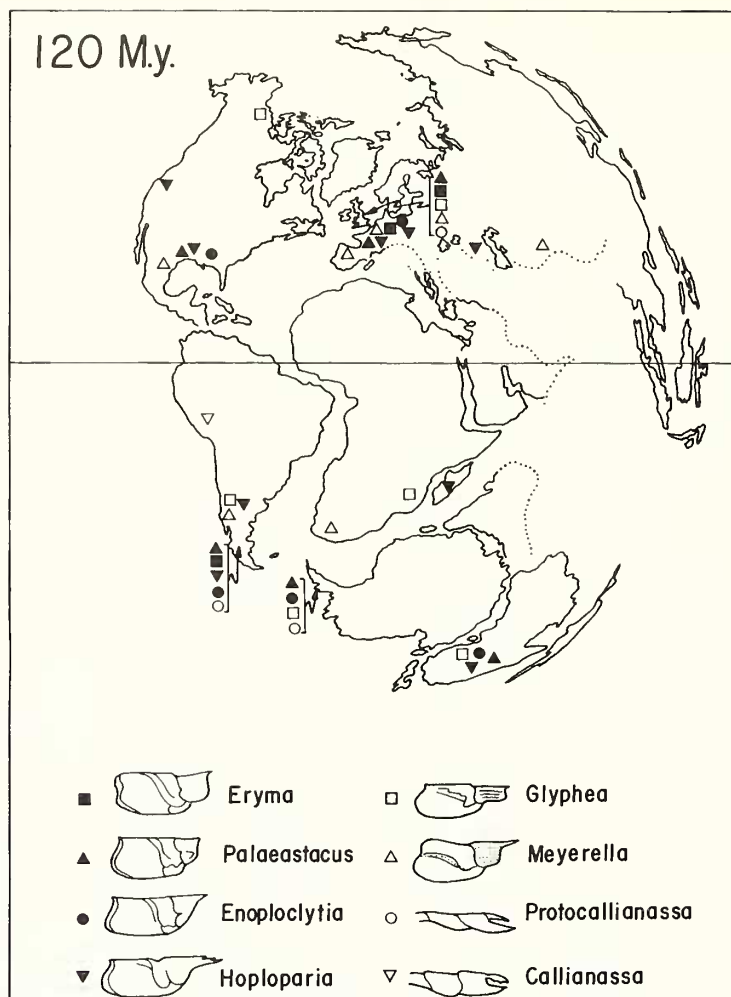
TEXT-FIG. 20. Palaeogeographic reconstruction showing the distribution of different genera during the Jurassic. Base map from Smith and Briden (1977) at 160 m.y. B.P. (Oxfordian).

of them, *Meyerella*, is exclusively Cretaceous. Another (*Protocallianassa*) is nearly restricted to that period. The rest can be separated in two groups: one with a previous history in the Jurassic (*Eryma*, *Palaeastacus*, *Glyphea*), and the other with representatives in the Tertiary (*Enoplocyrtia*, *Hoploparia*, *Callianassa*).

In the reconstruction of the Jurassic the world-wide distribution of *Eryma*, the root stock of *Palaeastacus* and *Enoplocyrtia*, is evident, while in the Cretaceous *Eryma* tends to diminish in distribution and dies out by the end of the period. *Palaeastacus* is geographically restricted in the Jurassic and becomes more widespread in Cretaceous times. As interpreted here, *Enoplocyrtia* is a genus mostly confined to the Cretaceous, with few representatives in the early Tertiary of North America.

Hoploparia flourished in the Cretaceous and continued to evolve in the early Tertiary, giving place to *Homarus*, a genus that is presently represented by few species. I think that the Cretaceous was a time of competition between nephropids and erymids, both filling similar ecologic niches, with a decline of the erymids which nearly disappeared by the end of the Cretaceous. During the Tertiary competition with the Brachyura caused the nephropids, in turn, to be reduced (Glaessner 1969).

As happens with *Eryma*, *Glyphea* is a very common Jurassic genus (poorly known in South America except for one record, Damborenea and Manceñido 1987) that declined in the Cretaceous, a trend which affected the whole family, as the Glypheidae nearly died out in the Eocene and are presently known by the 'living fossil' *Neoglyphea inopinata*.



TEXT-FIG. 21. Palaeogeographic reconstruction showing the distribution of different genera during the early Cretaceous. Base map from Smith and Briden (1977) at 120 m.y. B.P. (Barremian–Aptian boundary).

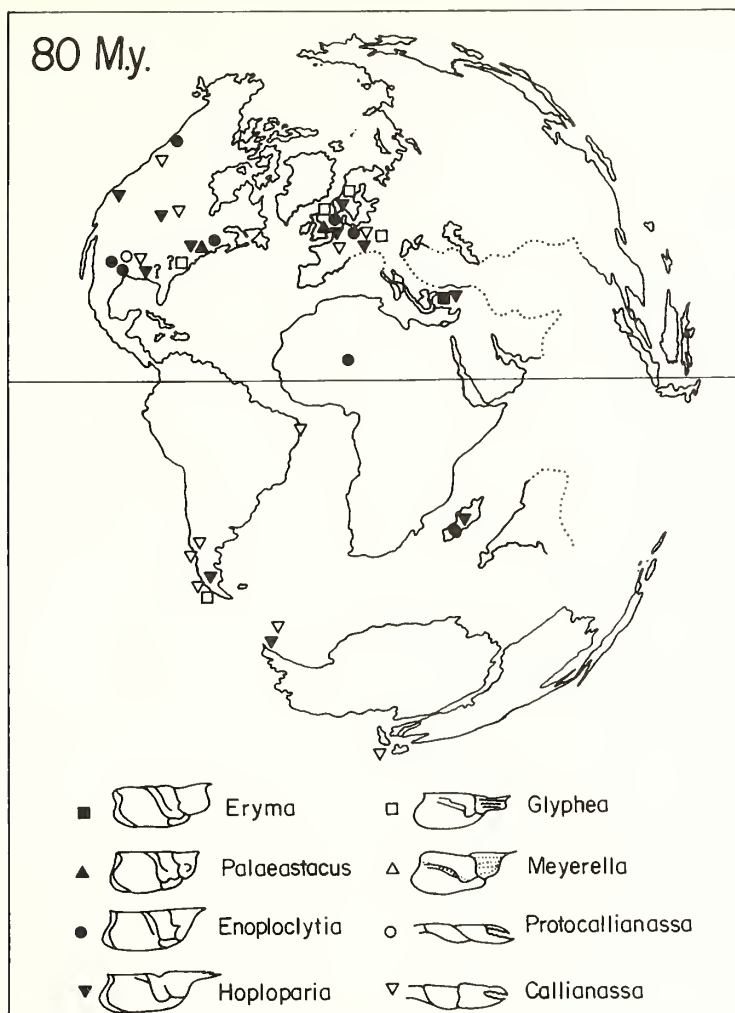
Meyerella is poorly known up to now and is most probably restricted to the early Cretaceous. As interpreted here, both *Protocallianassa* and *Callianassa* are known in Cretaceous rocks, the former nearly disappearing at the Cretaceous–Tertiary boundary. *Callianassa*, as a result of its particular mode of life, survived to the present, with a limited ecological niche (Glaessner 1957), but with a cosmopolitan distribution.

CONCLUDING REMARKS

The main conclusions of this study can be summarized as follows.

Sixteen species of fossil decapod crustaceans have been identified from Cretaceous rocks of Argentinian basins. They are representative of six families and their age ranges from Berriasian–early Valanginian to Maastrichtian–Danian (Tertiary).

Three different broad assemblages can be differentiated: (a) a Neocomian association mainly composed of Glypheidae and Mecochiridae from the Neuquén Basin; (b) a late lower Cretaceous



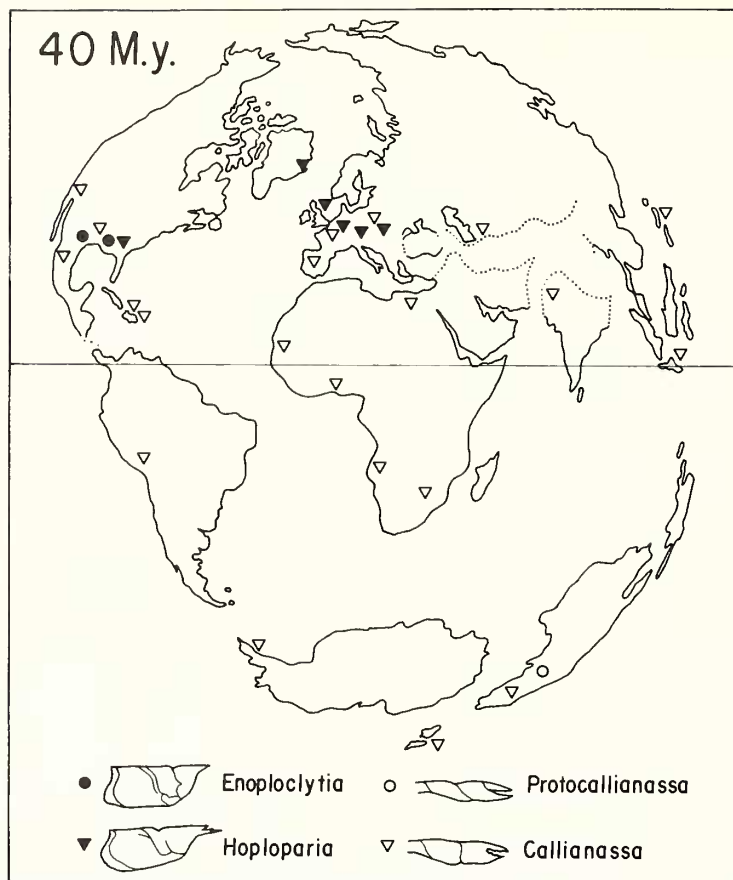
TEXT-FIG. 22. Palaeogeographic reconstruction showing the distribution of different genera during the late Cretaceous. Base map from Smith and Briden (1977) at 80 m.y. B.P. (Middle Campanian).

(s.l.) assemblage represented by the Erymidae, which occurs in the Austral Basin. (c) a late Cretaceous one, dominated by nephropids and callianassids; partially represented in the Neuquén, Austral and eastern Antarctic Basins.

The affinities of the species described are nearly world-wide, not restricted to the Caucasic-Indo-Pacific, as is true of most of the associated ammonite fauna.

No brachyuran decapods are presently known from Cretaceous rocks of southern South America and Antarctica, in sharp contrast to the dominantly brachyuran assemblages of the late Cretaceous of North America. However, I believe that this is partly due to collection failure.

With the exception of specimens of *Palaeastacus terraereginae* and *Callianassa burckhardti*, the latter (and probably the former) being associated with trace fossils, most of the species and specimens described here were recovered from calcareous nodules. They indicate an off-shore, low energy environment, with quiet sedimentation and anaerobic conditions. I consider their presence in that environment as allochthonous, with probable transport from littoral to sublittoral zones.



TEXT-FIG. 23. Palaeogeographic reconstruction showing the distribution of different genera during the early Tertiary. Base map from Smith and Briden (1977) at 40 m.y. B.P. (late Eocene).

Some of them also represent moulted skeletons. It is worth noting here that other benthic fauna is almost absent, as can be seen from the associated fauna given in the list of fossil localities.

The diversity of fossil decapod crustaceans recognized, as well as their wide geographic and stratigraphic distribution in the Argentinian Cretaceous basins, promote them as one of the most important decapod assemblages of the Southern Hemisphere.

Acknowledgements. I am indebted to the following colleagues who generously provided specimens for this study. M. Hünicken (Universidad de Córdoba), A. Riccardi (Museo de La Plata), F. Medina, E. Olivero (CIRGEO), A. Gutiérrez (Yacimientos Petrolíferos Fiscales), A. López Angriman (Universidad de Buenos Aires), and P. Rawson (University College, London). I would also like to acknowledge the valuable cooperation in the field of E. Roller, A. Riccardi (Museo de La Plata), V. Ramos, J. Płoszkiewicz, M. Palma, G. Marín and E. Perea (Servicio Geológico Nacional), H. Klinger (South African Museum), and to G. Pando (Yacimientos Petrolíferos Fiscales) for access to the scanning electron microscope. R. Allmendinger (Cornell University), the late R. Förster (Bayerische Staatssammlung für Paläontologie und historische Geologie), and S. Secretan (Muséum National d'Histoire Naturelle) for providing literature, M. E. Aguirre Urreta and P. Kress helped with French and German translations, G. Lo Forte prepared the diagrammatic reconstructions, L. Kilian copied most of the photographs for this paper, and L. Benialgo prepared the latex casts.

The author is most grateful to Professor Dr M. Glaessner (University of Adelaide), the late Dr R. Förster and Dr R. Feldmann (Kent State University) for criticism of an early version of the typescript.

The Consejo Nacional de Investigaciones Científicas y Técnicas of Argentina provided the funds for this study.

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Typescript received 8 December 1987

Revised typescript received 14 November 1988